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RHYSODINI OF THE WORLD
PART IV. REVISIONS OF RHYZODIASTES FAIRMAIRE AND CLINIDIUM KIRBY,
WITH NEW SPECIES IN OTHER GENERA (COLEOPTERA: CARABIDAE OR
RHYSODIDAE)

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ABSTRACT

This paper is fourth of a series which will constitute a revision of Rhysodini of the world. Rhyzodiastes Fairmaire and Clinidium Kirby are revised. New subgenera of Rhyzodiastes are: Rhyzotetrops NEW SUBGENUS, type-Rhyzodiastes janus, n. sp., one sp., Fiji; Rhyzoarca NEW SUBGENUS, type-Rhyzodiastes montrouzieri (Chevrolat), three spp. Australia, New Zealand, New Caledonia; Temoana NEW SUBGENUS, type-Rhyzodiastes spissicornis (Fairmaire), 25 spp. Southeast Asia, Southwest Pacific; Rhyzostrix NEW SUBGENUS, type-Rhyzodiastes maderiensis (Chevrolat), five spp. S. America. Five species from South America remain in Rhyzodiastes s. str.

The following new species are described (type localities indicated): Rhyzodiastes (Rhyzotetrops) janus (FIJI, Viti Levu); Rhyzodiastes (Temoana) bipunctatus (SOLOMON ISLANDS, Guadalcanal, Mt. Austen); Rhyzodiastes (Temoana) indigens (SUMATRA, Si Rambê); Rhyzodiastes (Temoana) convergens (NEW BRITAIN, Gisiluve); Rhyzodiastes (Temoana) preorbitalis (THAILAND, Doi Suteh); Rhyzodiastes (Temoana) vadiceps (BORNEO?); Rhyzodiastes (Temoana) patruus (MALAYA, Johor, Sedili Kechil); Rhyzodiastes (Temoana) denticauda (SARAWAK, Mt. Murud); Rhyzodiastes (Temoana) propinquus (NICOBAR IS.); Rhyzodiastes (Temoana) bonsae (SUMATRA, Mt. Tenggamoes); Rhyzodiastes (Temoana) alveus (VIET NAM, Hoa Binh); Rhyzodiastes (Temoana) fossatus (VIET NAM, hills sw. of Kui Chau); Rhyzodiastes (Rhyzostrix) davidsoni (BRAZIL, Amazonas, Taruma Falls); Rhyzodiastes (Rhyzostrix) nitidus (BRAZIL, Santarem); Rhyzodiastes (Rhyzostrix) menieri (FRENCH GUIANA, Haut-Carsevenne); Rhyzodiastes (s. str.) pentacyclus (BRAZIL, Alto da Serra); Rhyzodiastes (s. str.) suturalis (BRAZIL, Espiritu Santo, Sooretama); Clinidium (Mexiclinidium) championi (GUATEMALA, Quiche Mtns.); Clinidium (Mexiclinidium) newtoni (MEXICO, Chiapas, Pueblo Nuevo); Clinidium (Mexiclinidium) halffteri (MEXICO, Vera Cruz, Amates); Clinidium (Mexiclinidium) balli (MEXICO, Hidalgo, 25.6 km n. of Zimapan); Clinidium (Mexiclinidium) triplehorni (MEXICO, 11.3 km n.e. of Jucala); Clinidium (Mexiclinidium) iviei (MEXICO, Oaxaca, 3.2 km s. of Cerra Pelon); Clinidium (s. str.) impressum (FRENCH GUIANA, Saint Laurent du

Maroni); *Clinidium* (s. str.) *hammondi* (COLOMBIA, Bogota); *Clinidium* (s. str.) *howdenorum* (TRINIDAD, Morne Bleu); *Clinidium* (s. str.) *jolyi* (VENEZUELA, Merida, La Azulita); *Clinidium* (s. str.) *alleni* (PANAMA, Cerro Jefe); *Clinidium* (s. str.) *whiteheadi* (PANAMA, Cerro Campana); *Clinidium* (s. str.) *trionyx* (DOMINICAN REP., Cazabita); *Clinidium* (s. str.) *dormans* (PANAMA, Chiriqui, Finca Lerida, near Boquete); *Clinidium* (s. str.) *penicillatum* (COLOMBIA, Dept. Valle, Represa Calima); *Clinidium* (s. str.) *segne* (VENEZUELA, Aragua, Rancho Grande); *Clinidium* (s. str.) *kochalkai* (COLOMBIA, Casa Antonio, Loma, Cebolleta, Sierra Nevada de Santa Marta); *Clinidium* (s. str.) *microfossatum* (MARTINIQUE); *Clinidium* (s. str.) *smithsonianum* (DOMINICA); *Clinidium* (s. str.) *bechyneorum* (VENEZUELA, Carabobo, Hac. Montero, Montalban); *Clinidium* (s. str.) *excavatum* (VENEZUELA, Carabobo, Montalban Oeste); *Clinidium* (s. str.) *pala* (VENEZUELA, Miranda, Guatopo Nat. Pk., 50 km se Caracas); *Clinidium* (s. str.) *humile* (NEW GRANADA (Colombia or Panama)); *Clinidium* (s. str.) *curvatum* (COLOMBIA, Santander del Norte, Oroque); *Clinidium* (s. str.) *crater* (PANAMA, Cerro Jefe, Azul Ridge); *Clinidium* (s. str.) *spatulatum* (PANAMA, Colon, Sta. Rita ridge); *Clinidium* (s. str.) *moldenkei* (COSTA RICA, Rincon de Osa); *Clinidium* (s. str.) *argus* (PHILIPPINES (?) Horns of Negros); *Dhysores biimpressus* (TANZANIA, Usumbura, Neu Bethel); *Kaveinga* (s. str.) *poggii* (D'ENTRECASTEAUX ISLANDS, Goodenough Is.); *Grouvellina hexadon* (COMORO IS., Mayotte, Mamouzou); *Yamatosa kryzhanovskiy* (VIET NAM, mts. n.e. of Thai Nguen); *Yamatosa Kabakovi* (VIET NAM, mountains of Sha-Pa Province); *Omoglymmius* (*Pyxiglymmius*) *opacus* (SUMATRA, Padang); *Omoglymmius* (s. str.) *gressitti* (NEW GUINEA, Wau, Mt. Missim.); *Omoglymmius* (s. str.) *craticulus* (NEW GUINEA, Moroka); *Omoglymmius* (s. str.) *largus* (NEW GUINEA, Fly R.); *Omoglymmius* (s. str.) *tolai* (NEW BRITAIN, Rabaul); *Omoglymmius* (*Laminoglymmius*) *perplexus* (SUMATRA); *Omoglymmius* (*Navitia*) *peckorum* (FIJI, Viti Levu, Nandarivatu).

Clinidium beccarii *Grouvelle* is removed from *Rhyzodiastes* and returned to *Clinidium* (s. str.). *Rhysodes punctatolineatus* *Grouvelle* is assigned to *Arrowina*.

RÉSUMÉ

Cet article est la quatrième d'une série qui constitueront une revue taxonomique des *Rhyzodini* du monde. On revisite les genres *Rhyzodiastes* Fairmaire et *Clinidium* Kirby. Les sous-genres nouveaux de *Rhyzodiastes* sont: *Rhyzotetrops* NOUVEAU SOUS-GENRE, type-*Rhyzodiastes janus*, n. sp., un sp., Fiji; *Rhyzoarca* NOUVEAU SOUS-GENRE, type-*Rhyzodiastes montrouzieri* (Chevrolat), trois sp. Australia, Nouvelle Zélande, Nouvelle Calédonie; *Temoana* NOUVELLE SOUS-GENRE, type-*Rhyzodiastes spissicornis* (Fairmaire), 25 spp. Asie de sud-est, Pacifique de sud-ouest; *Rhyzostrix* NOUVEAU SOUS-GENRE, type-*Rhyzodiastes maderiensis* (Chevrolat), cinq spp., America du Sud. Cinq species de l'Amerique du Sud restaient en *Rhyzodiastes* s. str.

On décrit les espèces nouvelles que voici (en indiquant pour chacune la localité du spécimen type): *Rhyzodiastes* (*Rhyzotetrops*) *janus* (FIJI, Viti Levu); *Rhyzodiastes* (*Temoana*) *bipunctatus* (ÎLES DE SOLOMON, Guadalcanal, Mt. Austen); *Rhyzodiastes* (*Temoana*) *indigens* (SUMATRA, Si Rambê); *Rhyzodiastes* (*Temoana*) *convergens* (NOUVELLE BRETAGNE, Gisiluve); *Rhyzodiastes* (*Temoana*) *preorbitalis* (THAILAND, Doi Sute); *Rhyzodiastes* (*Temoana*) *vadiceps* (BORNEO?); *Rhyzodiastes* (*Temoana*) *patruus* (MALAYA, Johor, Sedili Kechil); *Rhyzodiastes* (*Temoana*) *denticauda* (SARAWAK, Mt. Murud); *Rhyzodiastes* (*Temoana*) *propinquus* (ÎLES DE NICOBAR); *Rhyzodiastes* (*Temoana*) *bonsae* (SUMATRA, Mt. Tenggamoes); *Rhyzodiastes* (*Temoana*) *alveus* (VIET NAM, Hoa Binh); *Rhyzodiastes* (*Temoana*) *fossatus* (VIET NAM, sur les collines au sud-ouest de Kui Chau); *Rhyzodiastes* (*Rhyzostrix*) *davidsoni* (BRÉSIL, Amazonas, Sault de Taruma); *Rhyzodiastes* (*Rhyzostrix*) *nitidus* (BRÉSIL, Santarem); *Rhyzodiastes* (*Rhyzostrix*) *menieri* (GUYANE FRANÇAISE, Haut-Carsevenne); *Rhyzodiastes* (s. str.) *pentacyclus* (BRÉSIL, Alto da Serra); *Rhyzodiastes* (s. str.) *suturalis* (BRÉSIL, Espiritu Santo, Sooretama); *Clinidium* (*Mexiclinidium*) *championi* (GAUTEMALA, Quiche Mtns.); *Clinidium* (*Mexiclinidium*) *newtoni* (MEXIQUE, Chiapas, Pueblo Nuevo); *Clinidium* (*Mexiclinidium*) *halffteri* (MEXIQUE, Vera Cruz, Amates); *Clinidium* (*Mexiclinidium*) *balli* (MEXIQUE, Hidalgo, 25.6 km n. de Zimapan); *Clinidium* (*Mexiclinidium*) *triplehorni* (MEXIQUE, 11.3 km n.e. de Jacala); *Clinidium* (*Mexiclinidium*) *iviei* (MEXIQUE, Oaxaca, 3.2 km s. de Cerra Pelon); *Clinidium* (s. str.) *impressum*

(*GUYANE FRANÇAISE, Saint Laurent du Maroni*); *Clinidium* (s. str.) *hammondi* (*COLOMBIE, Bogota*); *Clinidium* (s. str.) *howdenorum* (*TRINITÉ, Morne Bleu*); *Clinidium* (s. str.) *jolyi* (*VENEZUELA, Merida, La Azulita*); *Clinidium* (s. str.) *alleni* (*PANAMA, Cerro Jefe*); *Clinidium* (s. str.) *whiteheadi* (*PANAMA, Cerro Campana*); *Clinidium* (s. str.) *trionyx* (*REP. DOMINICAINE, Cazabita*); *Clinidium* (s. str.) *dormans* (*PANAMA, Chiriqui, Finca Lerida, près de Boquete*); *Clinidium* (s. str.) *penicillatum* (*COLOMBIE, Dept. Valle, Represa Calima*); *Clinidium* (s. str.) *segne* (*VENEZUELA, Aragua, Rancho Grande*); *Clinidium* (s. str.) *kochalkai* (*COLOMBIE, Casa Antonio, Loma Cebolleta, Sierra Nevada de Santa Marta*); *Clinidium* (s. str.) *microfossatum* (*MARTINIQUE*); *Clinidium* (s. str.) *smithsonianum* (*DOMINICA*); *Clinidium* (s. str.) *bechyneorum* (*VENEZUELA, Carabobo, Hac. Montero, Montalban*); *Clinidium* (s. str.) *excavatum* (*VENEZUELA, Carabobo, Montalban Oeste*); *Clinidium* (s. str.) *pala* (*VENEZUELA, Miranda, Guatopo Nat. pk., 50 km se Caracas*); *Clinidium* (s. str.) *humile* (*NEW GRANADA (Colombie ou Panama)*); *Clinidium* (s. str.) *curvatum* (*COLOMBIE, Santander del Norte, Oroque*); *Clinidium* (s. str.) *crater* (*PANAMA, Cerro Jefe, Azul Ridge*); *Clinidium* (s. str.) *spatulatum* (*PANAMA, Colon, Sta. Rita ridge*); *Clinidium* (s. str.) *moldenkei* (*COSTA RICA, Rincon de Osa*); *Clinidium* (s. str.) *argus* (*PHILIPPINES (?) Horns of Negros*); *Dhysores biimpressus* (*TANZANIA, Usumbura, Neu Bethel*); *Kaveinga* (s. str.) *poggii* (*ÎLES D'ENTRECASTEAUX, Goodenough Is.*); *Grouvellina hexadon* (*ÎLES COMORES, Mayotte, Mamouzou*); *Yamatosa kryzhanovskyi* (*VIET NAM, Monts du nord est de Thai Nguen*); *Yamatosa kabakovi* (*VIET NAM, Monts de la province de Sha-Pa*); *Omoglymmius* (*Pyxiglymmius*) *opacus* (*SUMATRA, Padang*); *Omoglymmius* (s. str.) *gressitti* (*NOUVELLE GUINÉE, Wau, Mt. Missim.*); *Omoglymmius* (s. str.) *craticulus* (*NOUVELLE GUINÉE, Moroka*); *Omoglymmius* (s. str.) *largus* (*NOUVELLE GUINÉE, Fly R.*); *Omoglymmius* (s. str.) *tolai* (*NOUVELLE BRETAGNE, Rabaul*); *Omoglymmius* (*Laminoglymmius*) *perplexus* (*SUMATRA*); *Omoglymmius* (*Navitia*) *peckorum* (*FIJI, Viti Levu, Nandarivatu*).

On deplacet Clinidium beccarii Grouvelle de Rhyzodiastes et le retourne a Clinidium (s. str.). *On attribuet Rhysodes punctatolineatus Grouvelle a Arrowina.*

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INTRODUCTION

This paper, the fourth in a series of five, consists of revisions of the genera *Rhyzodiastes* Fairmaire and *Clinidium* Kirby, together with descriptions of new species in several of the genera treated in earlier parts of the series. The subgenera of *Rhyzodiastes* are named and defined.

SOURCES OF MATERIAL

The following abbreviations designate collections cited in this paper. The names in parentheses are the curators of the respective institutions.

AIM	Auckland Institute and Museum, New Zealand (K.A.J. Wise)
ALB	University of Alberta, Edmonton, Canada (G. E. Ball)
AMNH	American Museum of Natural History, New York (L. Herman)
AMS	Instituut voor Taxonomische Zoologie, Amsterdam, Netherlands (J. Duffels)
AP	U.S. Dept. of Agriculture, Harrisburg, PA (K. Valley)
ARK	University of Arkansas, Fayetteville (E. P. Rouse)
AU	S.F. Austin State University, Nacogdoches, Texas (W. W. Gibson)
BMNH	British Museum, Natural History, London (R. Pope)
BMS	Buffalo Museum of Science, NY (H. W. Charnley)
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii (G. Samuelson)
BPM	Barry P. Moore, Canberra City, Australia
BSL	Naturhistorisches Museum, Basel, Switzerland (W. Wittmer)
BSRI	Biosystematics Research Institute, Ottawa, Canada (A. Smetana)
CAG	U.S. Dept. of Agriculture, Sacramento, CA (F. G. Andrews)
CAS	California Academy of Sciences, San Francisco, CA (D. Kavanaugh)
CMP	Carnegie Museum of Natural History, Pittsburgh, PA (G. Wallace)
CNHM	Field Museum of Natural History, Chicago, IL (H. Dybas)
CU	Cornell University, Ithaca, NY (L. L. Pechuman)
DM	Dayton Museum, Ohio (A. J. Koestner)
DSIR	Department of Scientific and Industrial Research, Auckland, N.Z. (J. Watt)
DY	Daniel K. Young, E. Lansing, MI
FLA	U.S. Dept. of Agriculture, Gainesville, FL (R. Woodruff)
GA	University of Georgia, Athens, GA (C. L. Smith)
GEN	Museo Civico di Storia Naturale "G. Doria", Genoa (R. Poggi)
GVA	Muséum d'Histoire Naturelle, Geneva, Switzerland (I. Löbl)
GLP	Gary L. Peters, Corvallis, OR
HL	Harry J. Lee, Fairview Park, OH
IO	Iowa State University, Ames IA (R. Miller)
INPA	Instituto Nacional de Pesquisas de Amazônia, Manaus, Brazil (N. D. Penny)
ISNHS	Illinois State Natural History Survey, Urbana IL (M. Sanderson)
IU	Indiana University, Bloomington IN
KS	Karl Stephan, Tucson, AZ
KU	Kagoshima University, Japan
LA	Los Angeles County Natural History Museum, CA (C. L. Hogue)
LCC	Lincoln College, Canterbury, N.Z., (R.M. Emberson)
LEI	Rijksmuseum von Natuurlijke Historie, Leiden, Netherlands (J. Krikken)
LEN	Academy of Sciences, Leningrad USSR (O. Kryzhanovskij)
LS	Louisiana State University, Baton Rouge LA (J. B. Chapin)

LUN	Zoological Institute, Lund, Sweden (R. Danielsson)
MAI	Michael A. Ivie, Columbus, OH
MAY	University of Puerto Rico, Mayaguez (J. Ramos)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA (J. Lawrence)
MN	University of Minnesota, St. Paul MN (P. J. Clausen)
MNHB	Museum für Naturkunde der Humboldt-Universität, Berlin, DDR (F. Hieke)
MNHN	Muséum National d'Histoire Naturelle, Paris, France (A. Descarpentries)
MO	University of Missouri, Columbia MO (W. R. Enns)
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium (P. Basilewsky)
MSU	Michigan State University, E. Lansing MI
MZSP	Museu de Zoologia da Universidade de São Paulo, Brazil (U.R. Martins)
NC	North Carolina State University, Raleigh NC (D. A. Young)
NMNH	U.S. National Museum of Natural History, Washington, D. C. (T. Erwin)
NMNZ	National Museum of New Zealand, Wellington (R. G. Ordish)
NMW	Naturhistorisches Museum Wien, Austria (F. Janczyk)
OK	Oklahoma State University, Stillwater OK (W. A. Drew)
OS	Oregon State University, Corvallis OR (G. L. Peters)
OSFS	Oregon State Forest Sciences Collection, Corvallis OR
OSU	Ohio State University, Columbus OH (C. A. Triplehorn)
OUA	Ohio University, Athens, OH (H. Seibert)
PA	Academy of Sciences, Philadelphia, PA (D. C. Rentz)
PK	Paul Kittle, Southeast Missouri State University, Cape Girardeau
PU	Purdue University, Lafayette, IN
QW	Quentin Wheeler, Columbus, OH
RCG	R. C. Graves, Bowling Green, OH
SATO	Masataka Sato, Nagoya, Japan
SDA	U.S. Dept. of Agriculture, Brookings, SD (V. M. Kirk)
SI	Southern Illinois University, Carbondale, IL (J. E. McPherson)
TB	Thomas Barr, University of Kentucky, Lexington KY
UCB	University of California, Berkeley CA (J. A. Chemsak)
UCD	University of California, Davis CA
UD	University of Delaware, Newark DE (P. P. Burbutis)
UI	University of Illinois, Urbana IL (R. Selander)
UK	University of Kansas, Lawrence KS (G. W. Byers)
UL	University of Louisville, KY (C. V. Covell)
UM	University of Michigan, Ann Arbor, MI (I. J. Cantrall)
UN	University of Nebraska, Lincoln NB (B. C. Ratcliffe)
UNH	University of New Hampshire, Durham NH (D. Chandler)
UT	Utah State University, Logan, UT (W. J. Hanson)
UVM	University of Vermont, Zoology Department, Burlington, VT
UW	University of Wisconsin, Madison WI (J. R. Baker)
VEN	Universidad Central de Venezuela, Maracay (L. J. Joly)
VP	Virginia Polytechnic Institute, Blacksburg, VA (M. Kosztarab)
WR	William Rosenberg

Description.— Apical stylet of antenna acuminate; tufts of minor setae present on Antennal Segments VII-X; compound eye divided into two ocellus-like structures, one directed anteriolaterally, the other posterio-laterally; clypeal setae present; pronotum with median groove strongly dilated; inner carinae sloped gradually into paramedian grooves; latter glabrous except for pollinose strip along medial margin of outer carina; latter with row of setae; outer carina curved, rather narrow, of even width; elytron with intercalary stria present; intratubercular stria obsolete except for apex, which is impressed; all femora with many long setae. This subgenus is restricted to Fiji.

Only one species is known.

Rhyzodiastes (Rhyzotetrops) janus new species
(Figs. 1, 5, 9, 10)

Type Material.— HOLOTYPE male, labelled: "Vitlevu, Fiji, 6 M.W. Nandarivatu, Mba, IX-16-38, Coll. Y. Kondo" (BPBM). PARATYPES one male, same data as holotype (BPBM); one female, labelled: "Nandarivatu, Viti Levu, Fiji, IX-10-38, 3700', rotten log, coll. E. G. Zimmerman" (BPBM); one female, same locality and collector but dated "IX-6-38, 3600', beating shrubbery" (BPBM); one female, labelled: "Navai, Fiji Isl. Mann" (MCZ); one female, labelled: "Viti Levu, Fiji, Nandarivatu, W. M. Mann" (MCZ); one female, labelled: "Fiji, Viti Levu, Nandarivatu, 13-xi-74, coll. B. P. Moore" (BPBM).

Description.— 5.9–6.3 mm. Tuft of minor setae very small on Segment VII of antenna; those of VIII-X larger; basal setae of antennae on Segments VII-X; Segments I-IV with subapical pollinose bands; outer antennal segments nearly spherical; Segment XI wider than Segment X, and over twice as long as latter.

Head slightly longer than wide; median lobe very short, transverse, its tip obtuse, far anterior to eyes; antennal lobe glabrous, but divided by anterior pollinose extension of postantennal groove; temporal lobe 1.5 longer than wide, broadly rounded medially, with broad pilose fringe across basal margin; orbital groove broad, distinct, but incomplete posteriorly, its base just posterior to posterior eye; gena with vertical bar of pollinosity ending ventrad to space separating anterior and posterior eyes (Fig. 10); one temporal seta.

Pronotum with length/greatest width 1.5, unusually large compared to elytra, more than 0.55 as long and nearly as wide as elytra; widest near middle, sides rather weakly curved; apex truncate; base rounded; median groove broadly dilated, forming about 0.2 of pronotal width; median groove entirely glabrous; anterior median pit near to anterior margin; posterior median pit at basal 0.25 of length; both median pits pollinose, conspicuous; median groove posterior to posterior median pit rather deep, but clearly shallower than remainder of pit; inner carinae rather narrow, sloped gradually into paramedian groove except in basal 0.25, where separated from paramedian groove by vertical scarp; paramedian grooves broad, glabrous except for narrow pollinose scarp bounding outer carina; basal impression conspicuous, glabrous except for small circular pollinose impression at middle; basal impression bounded posteriorly by glabrous ridge which is continuation of outer carina; outer carina curved, convex, narrow, of nearly even width, row of nine to 12 setae present in pollinose median scarp of outer carina; marginal groove entirely absent; notopleural suture entirely pollinose; sternopleural groove entirely absent.

Elytra rather short, sides nearly parallel; parascutellar pits large but widely separated from one another; base of elytra without transverse pollinose band; Interval I flat; sutural stria fine, scarcely pollinose, with fine, widely separated punctures; Interval II somewhat convex, sloped laterally; parasutural stria finely punctate, narrowly pollinose, slightly deeper than sutural stria, curved medially at base, meeting sutural stria at apex; apical depression largely glabrous but with posteriolateral pollinose strip; Interval III convex, its base bent medially, forming prominent angle; intercalary or third stria deeper than parasutural stria, with moderately broad strip of pollinosity; Interval IV with medial margin distinct but lateral one obsolete, continuous posteriorly with subapical tubercle; intratubercular stria incomplete, entirely effaced in basal 0.33, for most of remainder represented by row of minute, widely spaced punctures, its apex impressed, pollinose; apical tubercles swollen, broadly in contact at suture; marginal stria complete, pollinose, linear, becoming dilated below apical tubercle; submarginal stria entire, extending to middle of Sternum V; intercalary stria with about 10 setae; impressed apex of intercalary stria with two or three setae; medial face of apical tubercle with one or two setae; marginal stria with continuous row of about 15 setae, these more closely spaced near apex. (Fig. 5)

Metasternum not sulcate; abdominal sterna with transverse sulci narrowly interrupted at midline; slight development of lateral pit on Sternum IV in both sexes (Fig. 9); tibia slender, posterior spurs slightly smaller than anterior ones; male with anterior tibia not dentate nor tuberculate; male trochanters not modified; calcaria small, acutely pointed.

The presence of an intercalary stria is unique within the genus, as is the strange divided eye. A similar eye has evolved independently in *Clinidium* (s. str.) *beccarii* and its relatives.

SUBGENUS *RHYZOARCA* NEW SUBGENUS

Type species.— *Rhyzodes montrouzieri* Chevrolat 1875

Description.— Tufts of minor setae present on antennal Segments VII-X; clypeal setae absent; eyes entire, narrowly crescentic; temporal, pronotal, elytral setae entirely absent; pronotum relatively broad, subquadrate, with lateral margins slightly curved; base, apex truncate; median groove linear or absent; anterior median pit absent; posterior median pit small, shallow or absent; paramedian grooves closest together at middle of length, strongly curved; each paramedian groove with large pilose pit at anterior and posterior end; disc of pronotum depressed between anterior lateral pits; outer carina oval, broad at middle, tapered both anteriorly and posteriorly; marginal, submarginal grooves absent; intercalary stria absent; metasternal sulcus absent in *R. montrouzieri*, *R. proprius*, ventral surface of *R. burnsi* not studied; female with shallow, lateral pits on abdominal Sternum IV; male front femur with ventral tooth; calcar small, acutely pointed.

This subgenus occurs in Australia, New Zealand, and New Caledonia.

Phylogeny.— Of the three species, *R. proprius* and *R. burnsi*, of New Zealand and Australia, respectively, are clearly more closely related than either is to *R. montrouzieri* of New Caledonia.

KEY TO SPECIES

- 1 Apex of intratubercular stria impressed; median groove of pronotum absent; median lobe of head very short *R. montrouzieri* (Chevrolat), p. 8
- 1' Apex of intratubercular stria obsolete, subapical and apical tubercles thus not separated; median groove of pronotum linear but distinct; median lobe of head longer 2
- 2 (1') Sutural stria absent except for extreme base; parasutural stria impressed, impunctate; posterior median pit absent *R. proprius* (Broun), p. 9
- 2' Sutural stria entire, impressed, coarsely punctate; parasutural stria coarsely punctate; posterior median pit small but distinct *R. burnsi* (Oke), p. 9

Rhyzodiastes (*Rhyzoarca*) *montrouzieri* (Chevrolat 1875) NEW COMBINATION
(Figs. 2, 8)

Rhyzodes montrouzieri Chevrolat 1875: 182.

Rhyzodiastes montrouzieri (Chevrolat) Bell and Bell 1978

Type Material.— We have not located type material for this species. It is easily recognized from the description and the type locality.

Description.— Length 5.0-7.5 mm. Median lobe of head short, its tip opposite anterior margin of eye; length of eye about 0.8 of length of temporal lobe.

Pronotum relatively short, length/greatest width 1.35; anterior angles acute, slightly prominent; lateral margin not sinuate anterior to hind angle; base of pronotum relatively narrow, its width about 0.8 of greatest width of pronotum; median groove entirely absent; posterior median pit represented by shallow pit.

Elytron without basal pollinosity; sutural stria fine, linear, pollinose, impunctate, its base dilated, (Fig. 8); its apical 0.66 entirely effaced; parasutural stria entire, deep, impressed, pollinose; intratubercular stria complete, impressed, impunctate, pollinose, its apex separating apical and subapical tubercles; marginal stria represented by row of minute punctures, its apex not impressed; hind calcar of male acute, its dorsal margin straight.

This species is easily recognized by the short median lobe of the head, the impressed apex of the intratubercular stria, and the absence of the median groove of the pronotum.

Distribution.— Confined to New Caledonia. We have seen the following specimens: 13 males, five females, Col des Roussettes, 450-550 m., 4-6-II-63, G. Kuschel, C. Yoshimoto, J. L. Gressitt (BPBM); one female, Hanna, Foret de Thi, VII-16-1958, B. Malkin (CNHM); six males, three females, Mt. Koghi, Foret de Thi, 530 m., 8-III-1961, J. Sedlacek (BPBM); five males, four females, Noumea, Aug. 27-1944, Wilfred Crabb (NMNH); one male,

Mt. Chapeau, Gendarme rain forest, 13-VIII-1944, J. C. Herron (OUA)

Rhyzodiastes (Rhyzoarca) proprius (Broun 1880) NEW COMBINATION
(Figs. 3, 6)

Rhysodes proprius Broun 1880: 216.

Rhysodes probius Lewis 1888 (error).

Clinidium (Rhyzodiastes) proprium (Broun) Grouvelle 1903.

Rhyzodiastes proprius (Broun) Bell and Bell 1978.

Type Material.— Not studied. According to the original description, the type locality is Parua, New Zealand, and there were three syntypes.

Description.— Length 6.0-8.0 mm. Median lobe of head elongate, its tip posterior to eye; eye small, about 0.5 of length of temporal lobe.

Pronotum moderately long, length/greatest width 1.45; anterior angles obtuse; lateral margin shallowly sinuate anterior to hind angles; base of pronotum very broad, scarcely narrower than greatest width; median groove fine, inconspicuous, slightly abbreviated at base; posterior median pit absent.

Elytron without basal pollinosity; sutural interval of most specimens with elongate, very finely pollinose depression just posterior to middle of elytron, in some of the smallest specimens this depression entirely absent; sutural stria represented only by scarp-like basal portion, remainder entirely absent; parasutural stria pollinose, impunctate, deep, entire, its middle 0.33 slightly dilated; intratubercular stria impressed, impunctate for most of its length, its apex obsolete, not separating apical and subapical tubercle; marginal stria absent except for short impressed apical portion which is ventrad to apical tubercle (Fig. 6); hind calcar of male with its dorsal side convex, its apex a small but sharp point.

This species is similar to the next, but is easily separated by the absence of the sutural stria.

Distribution.— Confined to the North Island of New Zealand. We have studied the following specimens: one female, Auckland, coll. E. S. Gourley, 1970 (DSIR); one female, Auckland, Orere Bush, rotten log, 10-1-1957 (DSIR); one female, Bayswater, 9-13, #381, T. Broun colln. (DSIR); one female, Clevedon, under log, 2-4-1956, coll. J. C. Watt (DSIR); one male, one female, Huia, Auckland, ex rotten kauuka stump, 4-2-66, coll. J. C. Watt (DSIR); two females, Little Barrier, 1913, 117, coll. H. Swale (BMNH); one male, one female, Pollok, Auckland, coll. P. & M. Johns, 7-1-1964 (LCC); one male, one female, Rawhiti, forest remnant, Bay of Islands, 4-1-1969, coll. K. A. J. Wise (AIM); one female, Spirits Bay, Waipuna Stream, 9-XI-67, coll. J. I. T. and J. McB., litter (DSIR); one male, Tiki-Tiki, 18-1-63 (NMNZ); one female, Waitakere, Waitemata Co., C. E. Clarke colln. (AIM); one female, Whangarei, 18-20-3-31, coll. E. S. Gourley (DSIR); one male, one female, Whangarei Heads, colln. C. E. Clarke (AIM); four males, Whangarei, Pukerui Hills, 21-11-44, coll. B. Given (DSIR); one male, Whangarei, Three Mile Bush, 24-11-44, coll. B. Given (DSIR); one male, Whangarei, Western Hills, 13-IX-1956, coll. R. A. Crowson (CAS); one male, two females, Whangarei, Whau Valley, 11-8-28, coll. Fairburn (DSIR).

Rhyzodiastes (Rhyzoarca) burnsi (Oke 1932) NEW COMBINATION
(Figs. 4, 7)

Rhysodes burnsi Oke 1932: 148-149.

Rhyzodiastes burnsi (Oke) Bell and Bell 1978.

Type Material.— HOLOTYPE, female, from AUSTRALIA: New South Wales, Mt. Wilson, in log with ants, coll. C. Oke. We have not studied the type, but have seen a good enlarged photograph of it, kindly sent by B. Moore.

Description.— (Based on the original description and the photograph.) Length 7 mm. (Chaetotaxy not studied.) Median lobe of head elongate, its tip opposite posterior margin of eye; eye larger than in *R. proprius*; temporal lobes more rounded posteriorly than in latter species; pronotum moderately long, length/greatest width about 1.4; front angles obtuse; lateral margin shallowly sinuate anterior to hind angles; base of pronotum very broad, only slightly narrower than greatest width; median groove distinctly impressed; posterior median pit distinct.

Sutural interval without pollinosity but second interval with small pollinose spot at apical fourth (Fig. 7); sutural stria and parasutural striae both distinctly impressed, coarsely punctate; intratubercular stria shallowly impressed, coarsely punctate; its apex obsolete, not separating subapical and apical tubercles; marginal stria absent; according to original description, metasternum is sulcate.

The well-developed sutural striae and the coarse punctures of the sutural and parasutural striae separate this species from *R. proprius*. Oke suggested that the enlarged anterior lateral pits of the pronotum are trichomes and that the species might be myrmecophilous. This has neither been confirmed nor disproven. If true of this species, it is probably true of the entire

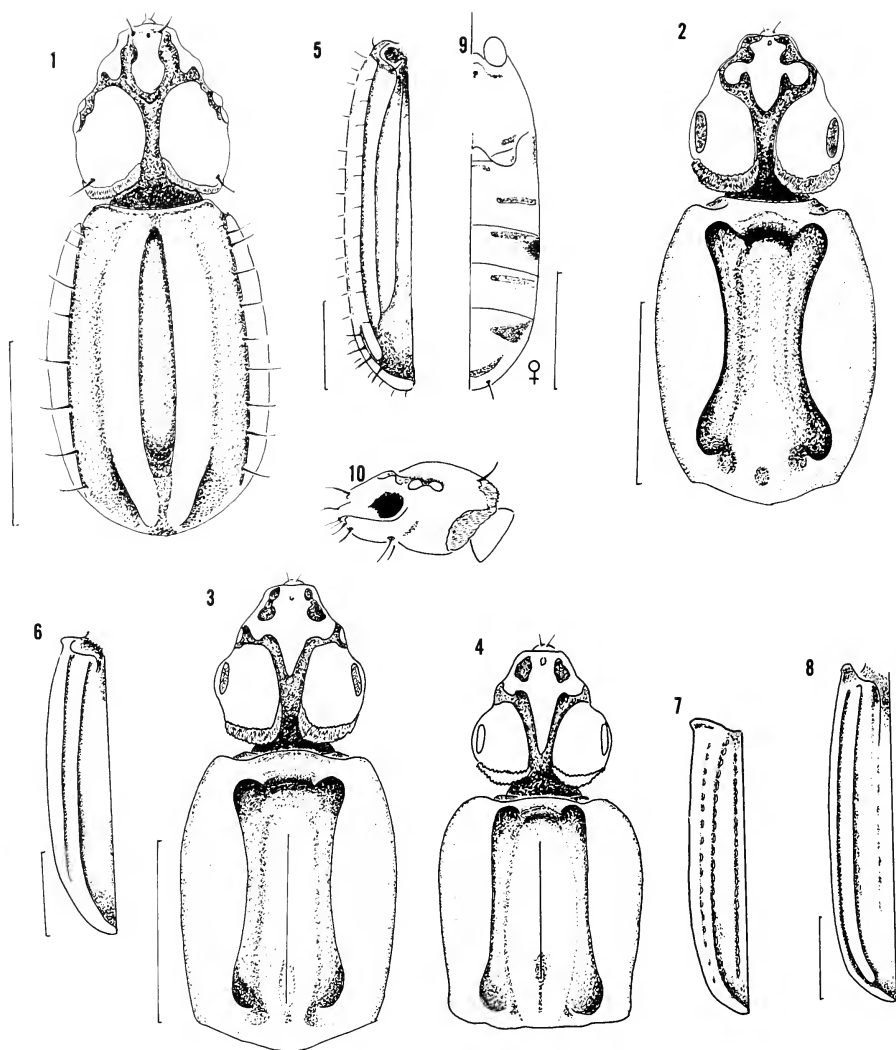


Plate 1. Figs. 1, 5, 9, 10. Genus *Rhyzodiastes*, new Subgenus *Rhyzotetrops* *R. (R.) janus* new species. Fig. 1, Head and pronotum, dorsal aspect; Fig. 5, Left elytron, dorsal aspect; Fig. 9, Metasternum and abdomen, left half; Fig. 10, Head, lateral aspect. Figs. 2-4, 6-8. Genus *Rhyzodiastes*, new Subgenus *Rhyzoarca*. Figs. 2-4, Head and pronotum, dorsal aspect; Fig. 2, *R. (R.) montrouzieri* (Chevrolat); Fig. 3, *R. (R.) proprius* (Broun) (drawn from photograph); Fig. 4, *R. (R.) burnsi* (Oke); Figs. 6-8, Left elytron, dorsal aspect; Fig. 6, *R. (R.) proprius* (Broun); Fig. 7, *R. (R.) burnsi* (Oke); Fig. 8, *R. (R.) montrouzieri* (Chevrolat).

subgenus.

SUBGENUS *TEMOANA* NEW SUBGENUS

Type species.— *Clinidium spissicorne* Fairmaire 1895.

Description.— Apical stylet of antenna present, though minute in some species; tufts of minor setae present on antennal Segments IV-X or V-X; clypeal setae present; compound eye narrow, crescentic; genae glabrous ventrad to eye; inner carinae of pronotum sloping gradually to paramedian groove; pollinosity on most species limited to border between paramedian groove and outer carina (more extensive in *R. pollinosus*); paramedian grooves straight or slightly curved; outer carina not greatly broadened at middle; elytron with intercalary stria absent.

This very large subgenus is most similar to *Rhyzotrix*, but lacks the enlarged eyes, the basal pollinosity of the pronotum and the genal pollinosity of the latter subgenus. In addition, all species of *Rhyzotrix* have coarsely punctate elytral striae. In *Temoana*, most species have the striae impunctate or nearly so, but *R. sulcicollis* is an exception, having strial punctures as coarse as those of *Rhyzotrix*.

Temoana ranges from the Caroline Islands, the Solomon Islands, and Australia westward to the Andaman Islands, eastern India, and Formosa.

Phylogeny.— We divide this large and complex subgenus into seven species groups as follows:

- I. *singularis* group - antennal tufts commence on Segment V; temporal setae present; orbital groove complete. Seven species, Australia, Solomon Islands, New Guinea, New Britain, Celebes, Formosa, Sumatra.
- II. *mishmicus* group - antennal tufts commence on Segment V; temporal setae absent; orbital groove reduced or absent. Three species, southeast Asia.
- III. *sulcicollis* group - antennal tufts commence on Segment V; marginal stria not impressed. Three species, Carolina and Molucca Islands.
- IV. *pollinosus* group - antennal tufts commence on Segment V; elytra extensively pollinose, with narrow raised carinae; three or more temporal setae. One species, Caroline Islands.
- V. *myopicus* group - antennal tufts begin on Segment IV; median groove of pronotum linear. Five species, Malay Peninsula, Borneo.
- VI. *gestroi* group - antennal tufts commence on Segment IV; median groove of pronotum moderately dilated. Three species, Sumatra, Andaman Islands.
- VII. *fairmairei* group - antennal tufts begin on Segment IV; median groove very strongly dilated. Three species, southeast Asia.

The interrelationships among these groups are not clear. The absence of an antennal tuft from Segment IV appears to us to be a plesiomorphic (primitive) character in the *singularis* and *sulcicollis* groups, since a low number of tufts (Segments VII-X) marks Subgenus *Rhyzotetrops*, which is the only Subgenus of *Rhyzodiastes* to retain the intercalary stria, and hence can be viewed as the most primitive *Rhyzodiastes*. In the related genus *Clinidium*, the least modified subgenera, *Arctoclinidium* and *Mexiclinidium* also have antennal tufts only on Segments VII-X, while in the most advanced Subgenus, *Clinidium s. str.*, most species have an increased number of tufts. It cannot be guaranteed, however, that the number of tufts has never decreased. In particular, the *mishmicus* group, without a tuft on Segment IV, shows close resemblances with the *myopicus* group which has such a tuft. The two groups are sympatric, and it is entirely possible that they are related, the tuft having secondarily been lost in the

former group. If this is true, then the *mishmicus*, *myopicus*, *gestroi*, and *fairmairei* groups might represent a single phyletic line, embracing all the species west of Wallace's Line. The *singularis* group is bound together mainly by characters which could be considered to be plesiomorphic, and perhaps it is not a true phyletic unit. *R. indigens*, which we provisionally place in the *singularis* group, is really very similar to *R. bonsae* of the *gestroi* group, and is perhaps an additional species which has secondarily lost the tuft from Segment IV. The monotypic *pollinosus* group is enigmatic. The pollinose surface and carinate intervals set it apart from all other *Temoana*. It appears superficially to be isolated, but it might be an offshoot of the *sulcicollis* group which has undergone extensive modification.

KEY TO SPECIES

- 1 Antennal tufts present on Segments V-X (absent from Segment IV) 2
- 1' Antennal tufts present on Segments IV-X 15
- 2 (1) Elytral intervals narrowly carinate; areas between carinae entirely
pollinose; orbital groove with one to three setae (*pollinosus* group)
..... *R. pollinosus* Bell and Bell, p. 14
- 2' Elytral intervals not narrowly carinate; pollinosity limited to narrow striae;
orbital groove with one seta or without (in one species, with one additional
temporal seta remote from orbital groove) 3
- 3 (2') Marginal stria of elytron not impressed (*sulcicollis* group) 4
- 3' Marginal stria impressed throughout its length 6
- 4 (3) Sutural stria of elytron impressed for basal 0.66 of its length; parasutural
stria with several setae *R. raffrayi* (Grouvelle), p. 15
- 4' Sutural stria not impressed, represented by row of coarse punctures or
entirely absent; parasutural stria without setae 5
- 5 (4') Sutural and marginal striae each represented by row of coarse punctures;
marginal groove of pronotum present *R. sulcicollis* (Grouvelle), p. 24
- 5' Sutural, marginal striae absent; marginal groove of pronotum absent
..... *R. maritimus* Bell and Bell, p. 25
- 6 (3') Orbital groove incomplete or absent; temporal seta absent (*mishmicus*
group) 7
- 6' Orbital groove complete; one or two temporal setae (*singularis* group) 9
- 7 (6) Orbital groove present, abbreviated at middle of eye
..... *R. mishmicus* (Arrow), p. 32
- 7' Orbital groove absent 8
- 8 (7') Metasternum sulcate *R. waterhousei* (Grouvelle), p. 33
- 8' Metasternum not sulcate *R. preorbitalis* new species, p. 34
- 9 (6') Sutural stria absent or represented only by a few punctures 10
- 9' Sutural stria impressed 11
- 10 (9) Median groove of pronotum obsolete; parasutural stria setose
..... *R. singularis* (Heller), p. 27
- 10' Median groove impressed; parasutural stria without setae
..... *R. guineensis* (Grouvelle), p. 26
- 11 (9') Two temporal setae present; one in center of lobe, one on orbital groove ..
..... *R. bipunctatus* new species, p. 28

11'	One temporal seta in orbital groove	12
12 (11')	Temporal lobes convergent posteriorly	
 <i>R. convergens</i> new species, p. 31	
12'	Temporal lobes not convergent posteriorly	13
13 (12')	Outer carina of pronotum strongly narrowed anteriorly, pronotum without distinct front angles; outer antennal segments twice as wide as long, cylindrical	
 <i>R. indigenus</i> new species, p. 31	
13'	Outer carina only slightly narrowed anteriorly, truncate at apex; pronotum with distinct front angles; outer segments sphaeroid, about 1.5 wider than long	14
14 (13')	Apex of pronotum slightly narrower than base; median groove dilated, as wide as anterior median pit; antennal Segments VIII-X with basal setae	
 <i>R. rimoganensis</i> (Miwa), p. 28	
14'	Apex of pronotum broader than base; median groove nearly linear, much narrower than anterior median pit; antenna without basal setae	
 <i>R. mirabilis</i> (Lea), p. 30	
15 (1')	Median groove linear between median pits (<i>myopicus</i> group)	16
15'	Median groove dilated between median pits	21
16 (15)	Parasutural stria straight to base; outer carina broad, truncate anteriorly	
 <i>R. myopicus</i> (Arrow), p. 37	
16'	Parasutural stria bent medially, crossing base of Interval II; outer carina narrow, not truncate anteriorly	17
17 (16')	Preapical tubercles not prominent, widely separated from one another; apical tubercle in lateral view not separated from preapical by deep notch	18
17'	Preapical tubercles prominent, tooth-like, separated from one another by width of sutural interval or less; apical tubercle in lateral view separated from preapical tubercle by deep notch	20
18 (17)	Pronotum without marginal groove; middle, hind tibiae each with two equal spurs, without curved apical process	
 <i>R. vadiceps</i> new species, p. 38	
18'	Pronotum with complete, pollinose marginal groove; middle, hind tibiae each with one spur, plus curved apical process laterad to spur	19
19 (18')	Temporal seta present; basal setae of antenna absent; ventral surfaces of femora of male tuberculate	
 <i>R. patruus</i> new species, p. 39	
19'	Temporal seta absent; basal setae of antenna present; ventral surface of femora of male not tuberculate	
 <i>R. frater</i> (Grouvelle), p. 38	
20 (17')	Apical tubercles contiguous; head as broad as long	
 <i>R. bifossulatus</i> (Grouvelle), p. 40	
20'	Apical tubercles widely separated from one another; head 1.5 longer than broad	
 <i>R. denticauda</i> new species, p. 41	
21 (15')	Median groove only moderately dilated, narrower than anterior median pit (<i>gestroi</i> group)	22
21'	Median groove very broadly dilated (<i>fairmairei</i> group)	24
22 (21)	Outer carina of pronotum broad, flat, sloped laterally; temporal lobes strongly convergent posteriorly	
 <i>R. gestroi</i> (Grouvelle), p. 42	
22'	Outer carina very narrow, strongly cariniform; temporal lobes not	

	convergent posteriorly	23
23	(22') Temporal lobes divergent posteriorly; cauda of elytra absent	
	<i>R. propinquus</i> new species, p. 43	
23'	Temporal lobes evenly rounded medially; cauda of elytra distinct	
	<i>R. bonsae</i> new species, p. 43	
24	(21') Median groove of pronotum dilated at middle, resembling keyhole; temporal seta absent	
	<i>R. fairmairei</i> (Grouvelle), p. 44	
24'	Median groove of pronotum long-oval; temporal seta present	25
25	(24') Metasternum sulcate; spurs of middle and hind tibiae equal; sutural, parasutural striae, Interval IV, apical tubercle setose	
	<i>R. spissicornis</i> (Fairmaire), p. 45	
25'	Metasternum not sulcate; tibial spurs very unequal; elytral setae limited to parasutural stria or absent	26
26	(25') Parasutural stria setose; deep portion of median groove six times longer than wide	
	<i>R. fossatus</i> new species, p. 47	
26'	Parasutural stria not setose; deep portion of median groove five times longer than wide	
	<i>R. alveus</i> new species, p. 46	

THE *POLLINOSUS* GROUP

The single species in this group differs from all other species of *Temoana* in having the elytron almost entirely pollinose except for three narrow glabrous carinae, and in having in most specimens more than one seta in the orbital groove.

Rhyzodiastes (Temoana) pollinosus Bell and Bell 1981 NEW COMBINATION
(Figs. 11, 19)

Rhyzodiastes pollinosus Bell and Bell 1981: 61-63.

Type Material.—HOLOTYPE male (CAROLINE ISLANDS), labelled: "Yap Group; Yap Island, Jul-Au 50, R. J. Goss" (BPBM). PARATYPES one male, same data as holotype; two females, one male, Yap Group, Gagil District; one male, Yap Group, Map I; two males, one female (on same point mount), Yap Group, Ruming I. All paratypes labelled: "July-Au 50, R. J. Goss" (BPBM).

Description.—Length 5.1-7.8 mm. Tufts of minor setae present on Segments V-X; median lobe of head short, broad, its tip anterior to eye; medial margin of temporal lobe curved; orbital groove very broad, pollinose, one to three temporal setae present in orbital groove.

Pronotum elongate, oval; length/greatest width 1.45; widest at basal 0.33; sides oblique anteriorly, evenly narrowed to apex, distinctly narrowed to base; hind angles very obtuse; base strongly oblique, forming obtuse angle at midline; pronotal setae absent; median groove relatively broad, closed anteriorly, open posteriorly; pollinose; paramedian groove very broad, sloped gradually to inner carina medially; outer carina curved, narrow, of even width; marginal groove not visible in dorsal view, not impressed, but represented by complete strip of pollinosity.

Elytron without distinct striae except for traces of sutural stria; each elytron with three narrow raised glabrous carinae, separated by broad pollinose areas (evidently representing dilated striae); elytron with many setae, about five medial to inner carinae; 10-12 between inner and second carinae; 12-14 between second and third carinae, and 15-20 between third carina and margin (Fig. 19); metasternum without median sulcus; Sterna III-V each with pair of broad pollinose transverse grooves; lateral pit in Sternum IV, slight in male, greatly enlarged in female; male with front and hind trochanters pointed; male anterior femur without ventral tooth; calcars of male pointed at apex, with dorsal margin sinuate or notched.

The narrow glabrous carinae on an otherwise pollinose elytron separate this species from all other members of the subgenus. The elytral carinae suggest *Rhyzodiastes s. str.* of South America, but the gradual lateral slope of the inner carina contrasts with the sharply defined lateral margin of the latter subgenus.

Distribution.— Caroline Islands. Recorded from Yap, Palau, and Ulithi. Detailed records are in Bell and Bell, 1981.

THE *SULCICOLLIS* GROUP

This group is characterized by the reduction of the marginal stria of the elytron, which is represented by a row of punctures or is entirely absent. The tufts of minor setae occur on antennal Segments V-X. The group is known from the Moluccas and the Caroline Islands. *R. sulcicollis* and *R. maritimus* appear closely related. Shared characters include: the outer carina of the pronotum is broad; the median groove is narrow and is abbreviated both anteriorly and posteriorly; the sutural stria is not impressed; the parasutural stria lacks setae. *R. raffrayi* is much more distantly related; as the outer carina of the pronotum is narrow and curved, the median groove is broader and is not abbreviated; the sutural stria is impressed for 0.67 of its length, and the parasutural stria has setae. All these characters are probably plesiomorphic, and *R. raffrayi* may be little modified from the common ancestor of the group. The two remaining species may have evolved from beetles similar to *R. raffrayi* which rafted to the Caroline Islands in the Equatorial Countercurrent. *R. maritimus* appears to have derived from populations from the central Carolines, which subsequently became *R. sulcicollis*, rather than representing a separate invasion from the Moluccas. In *R. pollinosus*, the form of the pronotum strongly suggests that of *R. raffrayi*, suggesting that the former species might be a highly modified offshoot of the latter species, and representing an independent invasion of the western Carolines.

Rhyzodiastes (Temoana) raffrayi Grouvelle 1895a NEW COMBINATION (Fig. 12)

Rhyzodiastes raffrayi Grouvelle 1895a: 158.

Clinidium raffrayi (Grouvelle) Grouvelle 1903.

Rhyzodiastes raffrayi (Grouvelle) Bell and Bell 1978.

Type Material.— HOLOTYPE male, labelled: "MOLUQUES: Gilolo, Raffray & Maindron, 78" (MNHN). This island is now known as Halmahera.

Description.— Length 5.3 mm. Antennal stylet short, pointed; tufts of minor setae present on Segments V-X; basal setae of antennal segments absent; Segment I with distinct apical pollinose band; Segments II-X without pollinosity; head longer than wide; median lobe pointed, its tip opposite anterior third of eye; postclypeal groove connected to frontal groove; medial margin of temporal lobe rather evenly curved; temporal lobes well separated from one another, coming closest together opposite posterior margin of eye; orbital groove entirely absent; one temporal seta present.

Pronotum only moderately elongate; length/greatest width 1.45; sides strongly curved, widest near middle; narrowed at base, apex; apex truncate; base rounded; hind angles very obtuse; median groove deep, moderately narrow, anterior median pit more dilated than posterior median pit; median groove deeply impressed to base; paramedian groove rather broad, its base dilated into large basal impression; basal impression closed posteriorly by raised glabrous carina which is continuous with outer carina; latter forms narrow, raised margin of uniform width, less than 0.2 of distance from paramedian groove to midline at middle of pronotal length; pronotal setae absent; marginal groove shallow, complete, visible only in lateral view.

Elytra elongate, slightly narrowed anteriorly; sutural stria fine, shallow, punctate; its apical third effaced; parasutural stria deep, complete, impunctate, its base bent medially to medial angle of scarp; intratubercular stria deep, impunctate, complete; marginal stria not impressed, represented by row of punctures, effaced in basal and apical thirds; apical portion of marginal stria impressed below apical tubercle; subapical and apical tubercles elevated; latter contacting one another at midline; parasutural stria with three setae in apical half; intratubercular stria with one or two setae near apex; apex of marginal stria with several setae; hind trochanter of male pointed; hind calcar of male bluntly pointed.

The above description is incomplete because the holotype is damaged, with the front legs missing. The female is unknown. The form of the pronotum is distinctive in this species, as is the combination of a reduced marginal stria with an impressed sutural stria which is 0.66

Plate 2. Figs. 11–21. Genus *Rhyzodiastes*, new Subgenus *Temoana*. Figs. 11–18. Head and pronotum, dorsal aspect; Fig. 11, *R. (T.) pollinosus* Bell and Bell; Fig. 12, *R. (T.) raffrayi* (Grouvelle); Fig. 13, *R. (T.) sulcicollis* (Grouvelle); Fig. 14, *R. (T.) maritimus* Bell and Bell; Fig. 15, *R. (T.) guineensis* (Grouvelle); Fig. 16, *R. (T.) singularis* (Heller); Fig. 17, *R. (T.) bipunctatus* new species; Fig. 18, *R. (T.) rimoganensis* (Miwa); Fig. 19, Left elytron, dorsal aspect, *R. (T.) pollinosus* Bell and Bell. Fig. 20, Hind tibia, male *R. (T.) guineensis* (Grouvelle). Fig. 21, Sternum VI, *R. (T.) bipunctatus* new species.

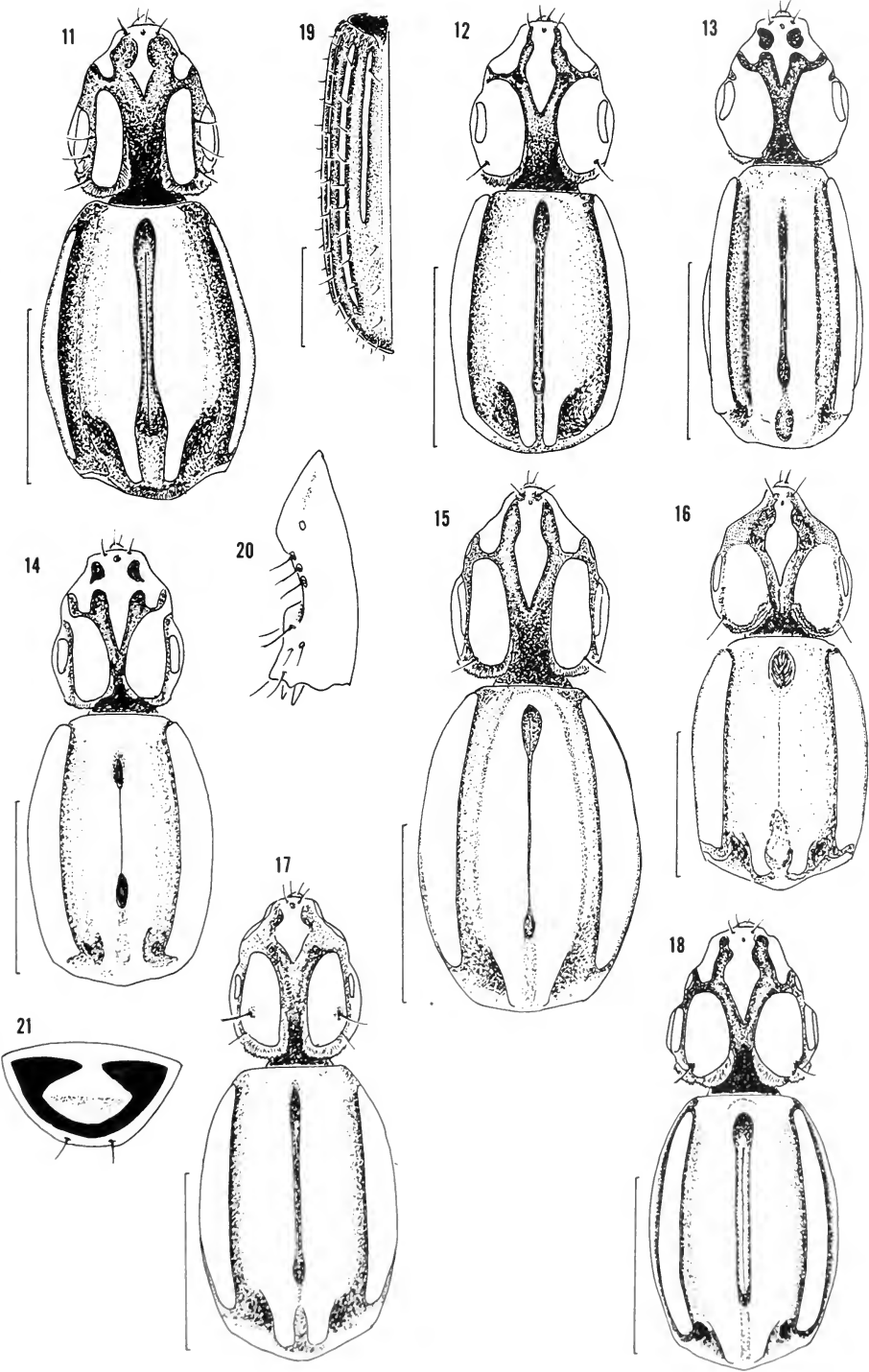


Plate 3. Figs. 22–33. Genus *Rhyzodiastes*, new Subgenus *Temoana*. Figs. 22–29, Head and pronotum, dorsal aspect; Fig. 22, *R. (T.) mirabilis* (Lea); Fig. 23, *R. (T.) indigens* new species; Fig. 24, *R. (T.) convergens* new species; Fig. 25, *R. (T.) waterhousei* (Grouvelle); Fig. 26, *R. (T.) mishmicus* (Arrow); Fig. 27, *R. (T.) myopicus* (Arrow); Fig. 28, *R. (T.) vadiceps* new species; Fig. 29, *R. (T.) preorbitalis* new species; Fig. 30, Sternum VI, *R. (T.) convergens* new species; Figs. 31–33, Sterna IV–VI, right half; Fig. 31, *R. (T.) preorbitalis* new species, female; Fig. 32, *R. (T.) myopicus* (Arrow), female; Fig. 33, *R. (T.) vadiceps* new species, male.

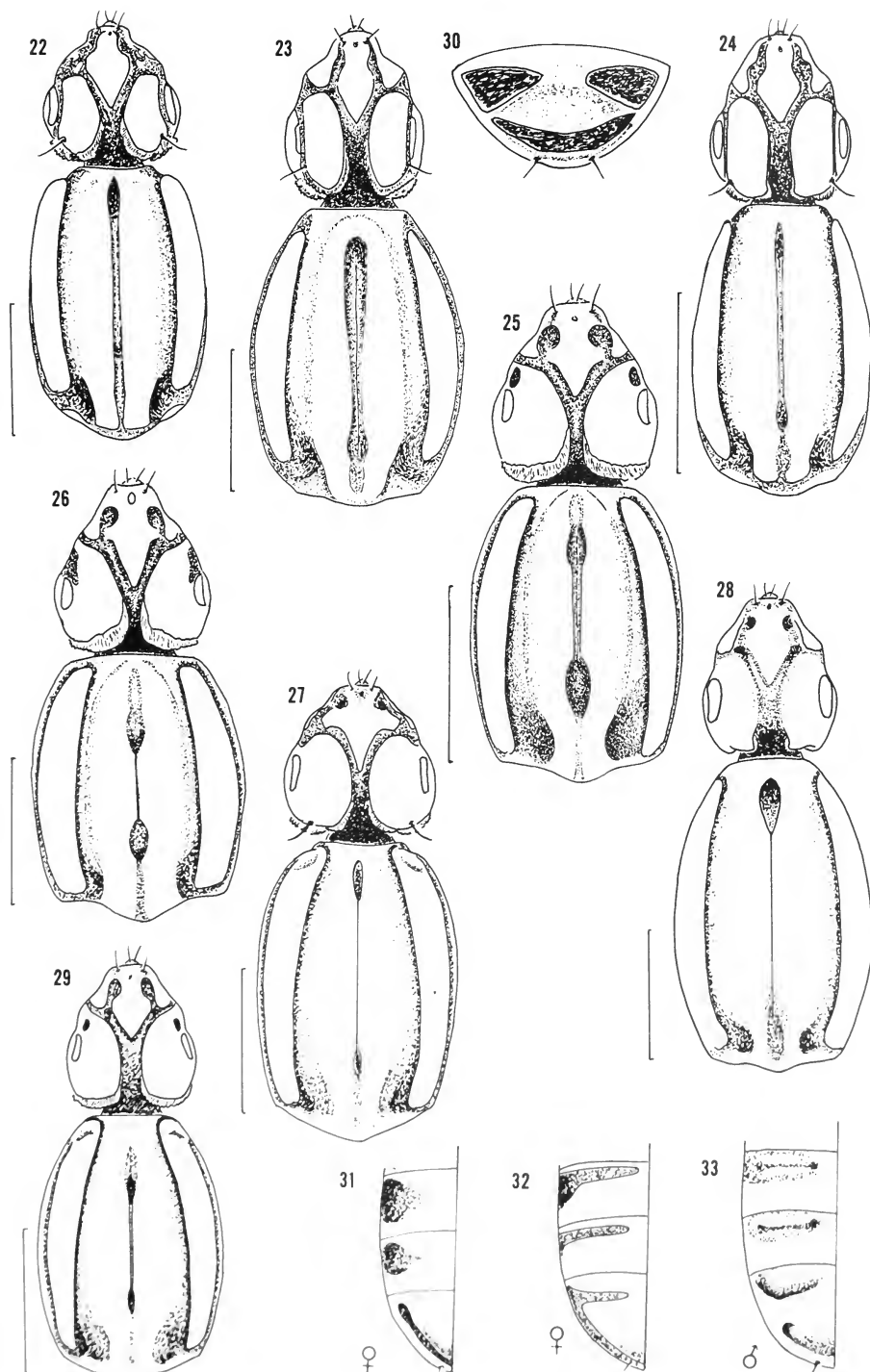


Plate 4. Figs. 34–45. Genus *Rhyzodiastes*, new Subgenus *Temoana*. Figs. 34–39, Head and pronotum, dorsal aspect; Fig. 34, *R. (T.) frater* (Grouvelle); Fig. 35, *R. (T.) patruus* new species; Fig. 36, *R. (T.) bifossulatus* (Grouvelle); Fig. 37, *R. (T.) denticauda* new species; Fig. 38, *R. (T.) gestroi* (Grouvelle); Fig. 39, *R. (T.) propinquus* new species; Figs. 40–41, Hind tibia, male; Fig. 40, *R. (T.) frater* (Grouvelle); Fig. 41, *R. (T.) patruus* new species; Figs. 42–43, Left elytron, apex, dorsal aspect; Fig. 42, *R. (T.) frater* (Grouvelle); Fig. 43, *R. (T.) patruus* new species; Figs. 44–45, Elytra, posterior aspect; Fig. 44, *R. (T.) bifossulatus* (Grouvelle); Fig. 45, *R. (T.) denticauda* new species.

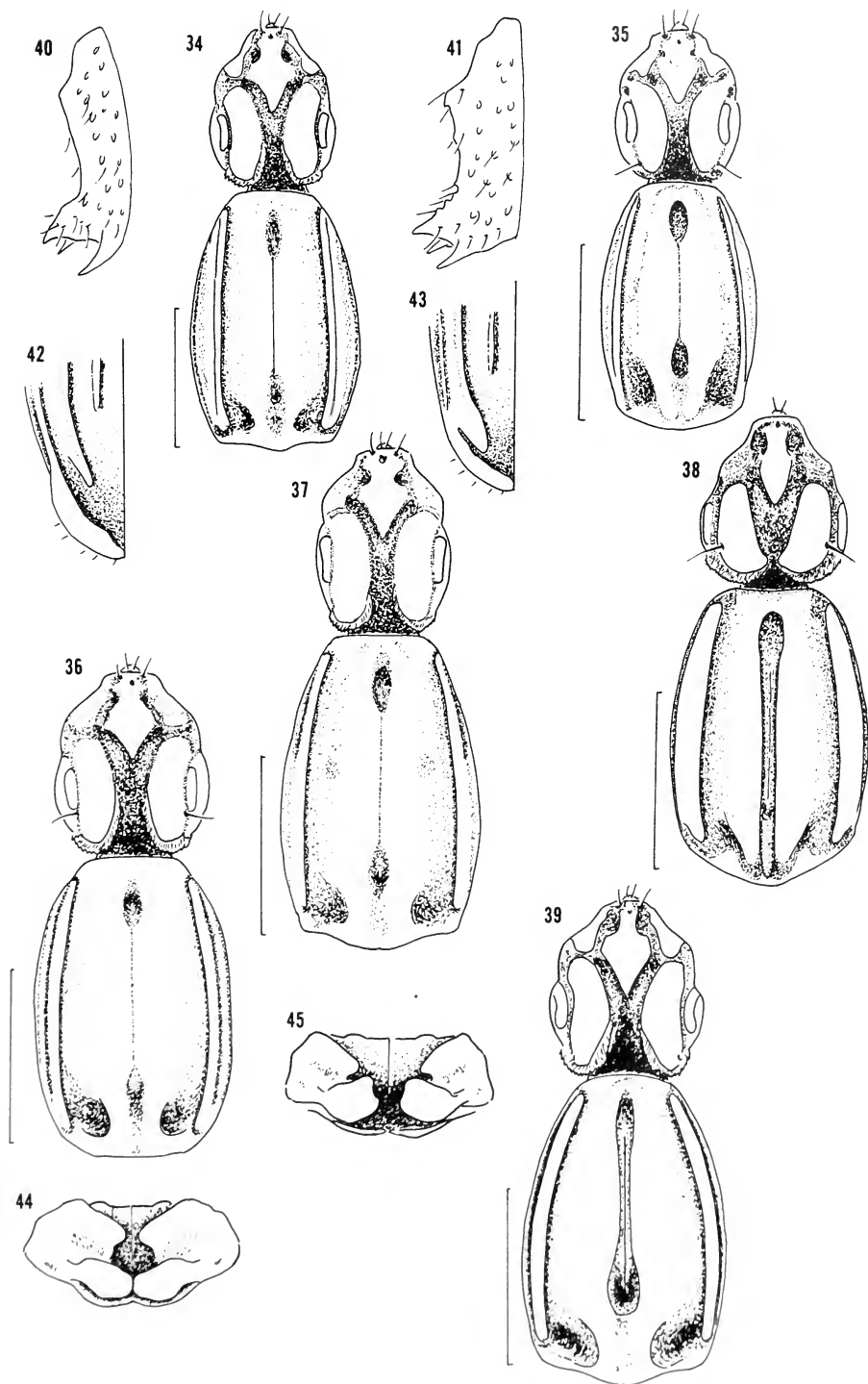
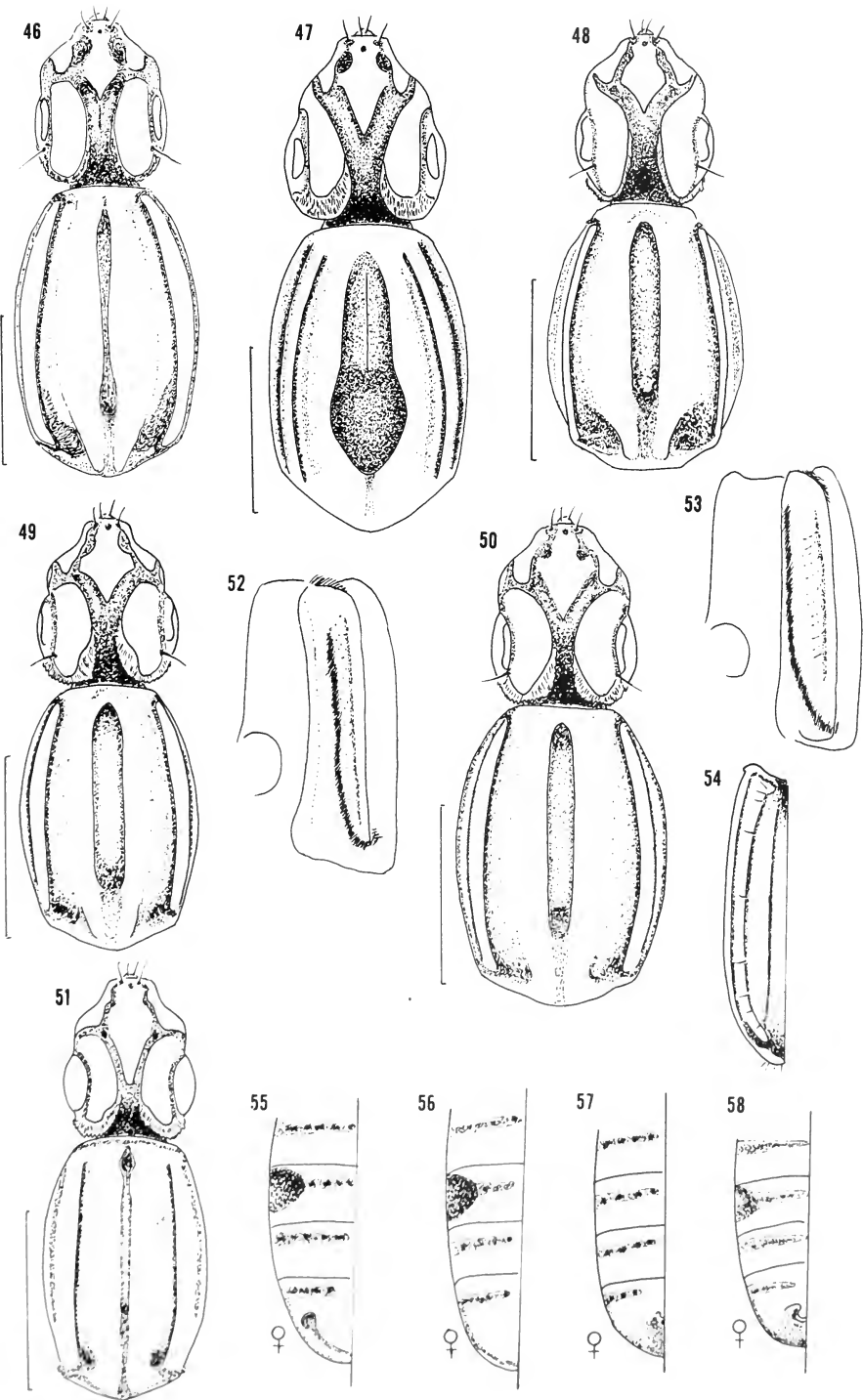


Plate 5. Figs. 46–50, 52–54. Genus *Rhyzodiastes*, new Subgenus *Temoana*. Figs. 46–51, Head and pronotum, dorsal aspect; Fig. 46, *R. (T.) bonsae* new species; Fig. 47, *R. (T.) fairmairei* (Grouvelle); Fig. 48, *R. (T.) spissicornis* (Fairmaire); Fig. 49, *R. (T.) alveus* new species; Fig. 50, *R. (T.) fossatus* new species; Figs. 52–53, Prothorax, left lateral aspect; Fig. 52, *R. (T.) alveus* new species; Fig. 53, *R. (T.) fossatus* new species; Fig. 54, Left elytron, dorsal aspect, *R. (T.) fossatus* new species. Figs. 51, 55–58. Genus *Rhyzodiastes*, new Subgenus *Rhyzostrix*. Fig. 51, *R. (R.) davidsoni* new species; Figs. 55–58, Sterna III–VI, right half, female; Fig. 55, *R. (R.) davidsoni* new species; Fig. 56, *R. (R.) nitidus* new species; Fig. 57, *R. (R.) menieri* new species; Fig. 58, *R. (R.) maderiensis* (Chevrolat).



complete.

Rhyzodiastes (Temoana) sulcicollis (Grouvelle 1903) NEW COMBINATION
(Fig. 13)

Clinidium sulcicolle Grouvelle 1903: 137-138.

Rhyzodiastes sulcicollis (Grouvelle) Bell and Bell 1981.

Type Material.— According to Grouvelle (1903), in the Oberthür collection. We did not find it in our visits to the MNHN, but it may be in recently discovered Oberthür material which we have not yet studied. Grouvelle gave the locality as "Isles Carolines: Hogolu" an obsolete name for Truk.

Description (abridged from Bell and Bell 1981).— Length 4.0-6.5 mm. Tufts of minor setae on Segments V-X; basal setae present on Segments V-X; Segment I with apical pollinose band; Segment II with trace of one; remaining segments without pollinosity; head slightly longer than wide; median lobe short, its tip acute, entirely anterior to eyes; median lobe narrowly connected laterally to antennal lobe, separating frontal groove from post-clypeal groove; latter forming isolated oval impression; temporal lobes rather narrowly separated at middle, forming obtuse median angles just posterior to posterior margin of eye; orbital groove entirely absent; small pollinose preorbital pit present; temporal setae absent; mentum with four prelabial and two labial setae.

Pronotum elongate, narrow, length/greatest width 1.65; widest near middle; lateral margin feebly curved, narrowed at apex, base; apex truncate, base rounded; hind angles very obtuse; pronotal setae absent; median groove very narrow, linear, its margins finely pollinose; groove closed at both ends, both median pits distinctly wider than groove, both removed from ends of groove, groove represented by shallow impressions anterior to anterior median pit and posterior to posterior median pit; posterior median pit equidistant from middle of pronotum and pronotal base (shallow median depression posterior to it looking like a second pit); paramedian groove narrow, posterior end with small, deep, punctiform basal impression; pollinosity of paramedian groove restricted to very narrow strip along lateral margin; inner carina with well-defined lateral margin, nearly straight, wider than paramedian groove; outer carina 0.66 as broad as inner carina at middle, curved, slightly tapered anteriorly; marginal groove entire, finely pilose, shallow except at posterior end.

Elytron slightly narrowed anteriorly; sutural stria not impressed, represented by row of very coarse punctures; parasutural and intratubercular striae deeply impressed; lateral margin of each higher than medial margin, suggesting a carina; parasutural and intratubercular striae uniting posteriorly; marginal striae not impressed except near apex; represented by row of very coarse punctures in middle of elytron, entirely effaced anteriorly and posteriorly; apex of marginal stria with four to six setae; elytron otherwise without setae; abdominal Sterna III-V each with pair of pollinose transverse sulci which are narrowly separated in midline, each with conspicuous puncture at medial end; a similar pair of pits but no transverse sulci on Sternum II; lateral ends of sulci of Sterna IV and V forming enlarged pits in both sexes, larger in female than in male; Sternum VI with submarginal groove and two pairs of anteriolateral pits; male without ventral tooth on anterior femur; trochanters of both sexes rounded; calcaria small, pointed. The male genitalia of this species have been illustrated by Bell and Bell (1978).

The coarse punctures of the sutural stria, which is not impressed, separate this species from all other members of the subgenus.

Bell and Bell (1981) discussed a form from the Islands of Param, Tol, and Dublon, which might be a separate species. In this form, the female is 4.0-5.0 mm. long, and lacks a tubercle of the sixth abdominal sternum. Females of the nominate form are 5.0-6.5 mm. long, and have a tubercle on the sixth sternum. This larger form coexists with the small one on the three islands named above, and is found in many additional islands. There is a male specimen, from Tol, which might belong to the dwarf form. It is only 4.0 mm. long, and has a pollinose spot near the center of the sixth sternum. All other males are larger, and have at least a trace of a tubercle at the middle of the sixth sternum. More collections are necessary to establish that the small male is correctly associated with the small female, and that the small form is a distinct species.

Distribution.— Central Carolines, on the high islands of Truk (Dublon, Moen, Tol, Param), also on the low island of Pis, in the barrier reef of Truk, and on the atolls of Satawal, Nama, and Woleai (Utagal Island). Bell and Bell (1981) consider it likely that the records from barrier islands and atolls result from accidental introduction by man. Bell and Bell (1981) give detailed locality records.

Rhyzodiastes (Temoana) maritimus Bell and Bell 1981 NEW COMBINATION
(Fig. 14)

Rhyzodiastes maritimus Bell and Bell 1981: 66-67.

Type Material.— HOLOTYPE female, labelled: KUSIAE, Mutunlik, 22 m. I-31-53, J.F.G. Clarke (BPBM). PARATYPES one female, same locality and collector as holotype; one female, KUSIAE: Mt. Matanta, 180 m., II-12-53, J.F.G. Clarke, "decaying *Hibiscus tiliaceus*" (BPBM).

Description (abridged from Bell and Bell 1981).— Length 4.3-6.2 mm. Tufts of minor setae present on Segments V-X; basal setae present on Antennal Segments V-X; Segment I with apical pollinose band which is interrupted ventrally; Segment II with trace of pollinosity dorsally; pollinosity otherwise absent from antenna; head distinctly longer than wide; median lobe rather long, ending in acute point opposite middle of eye; median lobe connected laterally to antennal lobe, separating postclypeal groove from frontal groove; postclypeal groove forming oval depression; temporal lobes converging posteriorly, closest together posterior to eyes, where they form rounded medial angles; orbital groove fine, linear, complete, extending to occiput; temporal seta absent; eye very narrow, crescentic, smaller than in related species; mentum with four prelabial and two postlabial setae.

Pronotum elongate, oval; length/greatest width 1.48, widest near middle, lateral margins distinctly curved, base slightly wider than apex; apex truncate, base rounded; hind angles very obtuse; pronotal setae absent; median groove very fine, linear, abbreviated both anteriorly and posteriorly, ending anteriorly at anterior median pit which is separated from anterior margin by more than its own length; median groove ending posteriorly at posterior median pit, which is closer to middle of pronotum than to base of pronotum; paramedian groove linear, curved, pollinose, ending posteriorly at basal impression, which is closed posteriorly; inner carina broad, flat, scarcely cariniform; outer carina about 0.5 as broad as inner one, of equal width throughout, curved; marginal groove entirely absent.

Elytron slightly narrowed anteriorly; sutural stria entirely absent; parasutural and intratubercular striae complete, impressed, finely punctate, pollinose; lateral margin of each stria much higher than medial margin, suggesting a carina; parasutural and intratubercular striae uniting posteriorly; marginal stria entirely absent except for a short impressed part near apex, which contains four to six setae; elytral setae otherwise absent; abdominal Sterna III-V each with transverse pollinose band which is narrowly interrupted at midline; Sternum II with pair of pollinose spots; Sternum VI with pair of transverse pollinose bands anteriorly, and an entire submarginal pollinose band posteriorly; female with lateral pit in Sternum IV (male unknown); midline of abdomen slightly carinate; femora entirely devoid of pollinosity and setae; trochanters and coxae glabrous.

This species is similar to *R. sulcicollis*, but is easily separated by the presence of the orbital groove, and the absence of the marginal groove of the pronotum and of the sutural and marginal striae.

Distribution.— Known only from Kusiae, in the eastern Caroline Islands.

THE SINGULARIS GROUP

In this group, the tufts commence on Antennal Segment V, the orbital groove and marginal striae are complete, and temporal setae are present. Six species are known, from Australia and the Solomon Islands, west to Celebes, Formosa, and Sumatra. In all species in which the male is known, the anterior and posterior trochanters are pointed in the male.

Phylogeny.— *R. guineensis* of New Guinea and *R. singularis* of Celebes appear to form a line apart from the other species. Among the characters shared by the two species are an obsolete median groove, an obsolete sutural stria and a last visible abdominal sternum with a narrow sub-marginal groove which is well separated from the transverse grooves. The male of *R. guineensis* differs from other known males in the form of the middle and hind tibiae, and in the presence of a tooth on the ventral margin of the anterior femur. The male of *R. singularis* is unknown, so it is uncertain whether or not these characters occurred in the common ancestor of it and *R. guineensis*.

In the remaining five species, the median prothoracic groove is deeply impressed, as is the sutural stria. In the male, the middle and hind tibiae are not thickened above the calcaria, and the anterior femur of the male is not toothed ventrally but is tuberculate in most species. The submarginal groove of Sternum VI is expanded and joined to the transverse groove, nearly

completely enclosing a diamond-shaped central glabrous area.

R. indigenus of Sumatra is a puzzling species. On one hand, it resembles *R. bonsae* of the *gestroi* group, also from Sumatra. It might be a relative of the latter species which has secondarily lost the tuft of minor setae on Segment IV. On the other hand, it is close to *R. mirabilis* of Australia (*singularis* group) except for the shape of the pronotum.

The four remaining species can be grouped in two pairs: *R. bipunctatus* of Guadalcanal and *R. rimoganensis* of Taiwan have many setae in the parasutural stria, and well developed basal setae on some of the outer antennal segments, and have at least some of the transverse sulci of the abdomen continuous across the midline; *R. mirabilis* of Australia and *R. convergens* of New Britain, have the parasutural stria with at most one seta, and lack basal setae on the antennal segments, while the transverse grooves are broadly separated at the midline.

Rhyzodiastes (Temoana) guineensis (Grouvelle 1903) NEW COMBINATION
(Figs. 15, 20)

Clinidium guineense Grouvelle 1903: 138-139.

Rhyzodiastes guineensis (Grouvelle) Bell and Bell 1978

Type Material.—LECTOTYPE (here designated) male, labelled: "Nuova Guinea, Fly River, L. M. D'Albertis, 1876-77" (GEN). PARALECTOTYPES 11 males, 11 females, same data as lectotype (GEN). In the original description, mention is also made of a specimen collected at Sattelberg by Biró, located in the Budapest Museum. We have not studied this specimen and cannot testify it is identical to the series from the Fly River. A male specimen in the BMNH is labelled "co-type, New Guinea 1901.267, N.J. Gella or Golla". This specimen is not listed in the original description and is probably incorrectly labelled as a co-type.

Description.—Length 6.3-8.0 mm. Antennal stylet small, acute, tufts of minor setae present on Segments V-X; Antennal Segments IX and X with basal setae; Segment I pollinose dorsally; Segment II with broken pollinose ring; Segment III with traces of pollinosity; head almost twice as long as wide; median lobe rhomboid, its apex acute, opposite middle of eye; median lobe separated from antennal lobe; latter shining, glabrous; temporal lobe 2.5 longer than wide; frontal space unusually long, wide; medial margins nearly straight; temporal lobe with rather broad fringe of pilosity on posterior margin and posterior 0.5 of medial margin; temporal lobes actually somewhat convergent posteriorly, but this is inconspicuous because it is concealed by the fringe; frontal grooves deep; postantennal grooves deep, entire, narrow; orbital groove deep, narrow, nearly straight, margin with postorbital pilosity shortly behind eye; temporal lobes separated by more than width of one of them; temporal lobe flat, shining, impunctate; eye narrow, crescentic, about twice as long as wide, 0.66 of length of temporal lobe; one temporal seta located in orbital groove just posterior to eye; genae glabrous.

Pronotum moderately long, length/greatest width 1.46; widest slightly behind middle, sides curved, base narrowed, apex more strongly narrowed; median groove very fine, linear between the pits; anterior median pit enlarged, tear-drop shaped, apical; posterior median pit at basal 0.25 of length, median groove posterior to it widened, shallow; median groove entirely glabrous; inner carinae together forming convex, glabrous surface, sloping laterally into paramedian groove; latter distinct, its floor glabrous, its lateral boundary (medial scarp of outer carina) pollinose; basal impression small, oblique, closed posteriorly by flat glabrous elevation; outer carina narrowed anteriorly, broadened posteriorly, its base rounded, apex very narrowly truncate; pollinosity of its medial margin attaining hind angle, curving into marginal groove; marginal groove complete, linear, not visible in dorsal view; pronotal setae absent, sub-marginal groove absent; propleuron iridescent; anterior part of notopleural suture pollinose; sternopleural groove absent; pleural groove represented by reduced pit.

Elytra rather narrow, scutellar pits very large, surrounded by pollinosity which meets at midline anterior to pits, forming triangle, tapering posteriorly to point at base of remnant of sutural stria, connected laterally to transverse strip which reaches base of parasutural stria; sutural stria reduced to short, medially-directed scarp in basal 0.2 of length; first and second intervals thus scarcely distinct; in some specimens a line of fine punctures represents more posterior part of sutural stria in middle 0.33 of elytron; parasutural stria straight, complete, forming pollinose, medially-directed scarp; Interval III nearly flat, facing dorsolaterally; basal pollinosity of elytron broadly interrupted opposite base of Interval III; apex of Interval III forming subapical tubercle which is not at all swollen; intratubercular stria linear, pollinose, impressed, its base disappearing into humeral pollinose area of elytron; apex of intratubercular stria merging with broad pollinose band across anterior walls of apical tubercles; marginal stria impressed, linear, pollinose, complete; apical tubercle impunctate, slightly swollen; elytron entirely without setae; metasternum not sulcate; transverse sulci of abdominal sterna narrowly separated at midline; female with lateral pits in Sternum IV; tibial spurs of middle and hind legs slightly unequal; male with trochanters I, III pointed; anterior femur of male with ventral tooth; calcaria with distinct shoulder tooth, bounded above by rounded emargination (Fig. 20); tibia above emargination greatly thickened.

The greatly reduced sutural stria separates this species from all others excepting *R. singularis*. From the latter species it differs in having the subapical tubercle narrow, in lacking elytral setae, and in having the median groove of the pronotum impressed, though narrow.

Distribution.— New Guinea. In addition to the type material, we have seen one female specimen, labelled: "NEW GUINEA, Orio, 145', Purari River, Oct. 7, 1967" (MCZ) and one female, labelled: "Humboldt B., N. Guinea, Doherty" (MNHN). This locality was later called Hollandia.

Rhyzodiastes (Temoana) singularis (Heller 1898) NEW COMBINATION
(Fig. 16)

Clinidium singulare Heller 1898: 3.

Rhyzodiastes singularis (Heller) Bell and Bell 1978.

Type Material.— HOLOTYPE female, labelled: "S. CELEBES, Lompa-Battau, 3000', März, 1896, H. Fruhstorfer, ex museo W. Rothschild, 1899" (MNHN).

Description.— Length 7.0 mm. Antennal stylet small, acute; antennal segments entirely without basal setae; all antennal segments with pollinose rings (these broken on Segments IX, X), tufts of minor setae on V-X; head only slightly longer than wide, median lobe hastate, rather short, its apex acute, opposite middle of eye; antennal lobe entirely pollinose; temporal lobe 1.5 longer than wide; frontal space broad, its anterior 0.5 glabrous except for linear median strip; frontal grooves deep but glabrous; medial margins of temporal lobes broadly curved, closest together opposite middle of eyes; temporal lobe with fringe of pilosity on posterior margin; frontal grooves deep, glabrous; orbital groove complete though very narrow opposite middle of eye; temporal lobe convex, shining, impunctate; eye small, crescentic, about 0.5 length of temporal lobe, its length three times its width; one temporal seta present, in orbital groove midway between hind margin of eye and occipital angle; genae glabrous.

Pronotum moderately long, length/greatest width 1.44; widest behind middle, sides curved, base and apex both only slightly narrowed; median groove obsolete, scarcely visible; anterior median pit large, tear-drop shaped, apical; posterior median pit large, occupying basal 0.15 of length, constricted at 0.5 of its length, open posteriorly; inner carinae fused to form broad convex glabrous surface, sloping laterally into paramedian groove; bases of inner carinae form lobes on either side of posterior median pit; margins of lobes fringed with pollinosity; basal impressions oblique, punctiform, pollinose, bounded posteriorly by flat glabrous ridges; paramedian groove bounded laterally by steep, pollinose, slightly undulated scarp; outer carina only slightly narrowed anteriorly, medial margin nearly straight, lateral one feebly curved; pollinosity of its medial margin attaining hind angle, curved into marginal groove; marginal groove complete, linear, scarcely visible in dorsal view; submarginal groove absent; pronotal setae absent; pollinose pit present at anterior end of notopleural suture; sternopleural groove absent; pleural groove oblique, narrow.

Elytron moderately narrow; pilose area occupying lateral part of base of sutural interval, nearly concealing scutellar pits; sutural stria almost absent, in basal 0.2 represented by medially-directed scarp, from there to middle of length barely traceable as a shallow impression; in posterior 0.5 of elytron entirely invisible; first and second intervals thus not distinct; parasutural stria straight, complete, forming pollinose, medially-directed scarp; basal transverse pollinosity of elytron entire, not interrupted opposite base of Interval III, Interval III convex, its apex forms strongly swollen subapical tubercle, medial margin of latter (apex of parasutural stria) abruptly sinuate; intratubercular stria impressed, linear, entire, its apex merging with broad pollinose band across anterior wall of apical tubercle; Interval IV continuous with apical tubercle, latter not swollen; marginal stria complete, linear, impressed, pollinose; parasutural stria with at least three or four setae near base perhaps with complete row of very small setae (only basal punctures visible in holotype, but it appears that setae may have broken off); intratubercular stria with one big basal seta; apical tubercle with several small setae; marginal stria with several setae in apical portion; metasternum not sulcate; transverse sulci of abdominal Sterna III-VI widely separated medially; female with rather small lateral pit in Sternum IV; Sternum VI with basal transverse sulci broadly separated from submarginal groove; middle of Sternum VI evenly convex.

This species is separated from all other except *R. guineensis* by the great reduction of the sutural stria. It differs from the latter in having well-developed elytral setae, in having the medial margin of the subapical tubercle strongly swollen, and in having the median groove of the pronotum almost absent.

Rhyzodiastes (Temoana) bipunctatus new species
(Figs. 17, 21)

Type Material.— HOLOTYPE male, labelled: "SOLOMON ISLANDS: Gaudalcanal, Mt. Austen, 18/4.1963, P. Greenslade, 5401, B.M. 1966-477" (BMNH). PARATYPES one male, same data as holotype except dated 19-9-1962 (BMNH); one female, labelled: "SOLOMON ISLANDS, Gaudalcanal, Ngali Mtn., 8/8,1963, P. Greenslade, 8383" (BMNH). There is another male, missing head and pronotum, that is mounted on the same pin as this specimen but it was not made a paratype.

Description.— Length 5.0-7.9 mm. Antennal stylet short, conical; tufts of minor setae on Segments V-X; antennal Segments VI-X with basal setae; antennal Segments I-X with pollinose rings (those of IX, X more or less broken between the setae); head longer than wide; median lobe short, triangular, its apex pointed, opposite anterior margin of eye; antennal lobe entirely pollinose; frontal space broad, parallel-sided pollinose; frontal grooves broad, deep, pollinose; temporal lobe 2.5 times longer than wide, entirely broadly fringed with pilosity; orbital groove broad, deep, continuous; two temporal setae present, one located in orbital groove near posterolateral angle of temporal lobe, the other arising from conspicuous puncture in glabrous part of temporal lobe well posterior to eye; eye narrow, crescentic, less than 0.5 length of temporal lobe; posterior 0.5 of gena pilose.

Pronotum moderately elongate, length/greatest width 1.50, widest at middle, sides distinctly curved; both ends narrowed, the apex more than the base; median groove deep, middle 0.33 sublinear; anterior median pit apical, dilated; posterior median pit appearing double, anterior portion at basal 0.33 of pronotum, this separated by constriction from posterior part which is almost as deep, and which reaches base of pronotum; median groove and pits pollinose; inner carina convex, glabrous, rather broad, its lateral margin more distinct from paramedian groove than in most species of *Temoana*; inner carina and paramedian groove without evident microsculpture; paramedian groove bounded laterally by broad pollinose strip along nearly vertical medial scarp on outer carina; basal impression oblique, pollinose, about 0.20 of length of pronotum; outer carina broad, its medial margin only slightly curved, its lateral margin more strongly so, therefore outer carina is widest at middle and tapered at both ends; marginal groove marked by complete strip of pollinosity, but little impressed, scarcely visible in dorsal view, but well-marked in lateral view; submarginal groove absent; pronotal setae absent; notopleural suture with pollinosity in anterior 0.5; sternopleural groove absent; pleural groove impressed, pollinose, its ventral 0.5 linear, its dorsal 0.5 expanded into a pit.

Elytra rather narrow, without a caudal lobe; scutellar pits present, but inconspicuous, lying within transverse band of pilosity which extends entirely across base of elytra; sutural interval flat; sutural stria with basal 0.25 glabrous, middle portion with pollinose strip, apex recurved for short distance at apical 0.25 of elytron; its apex not joining parasutural stria; Interval II nearly flat, sloped laterally; parasutural stria impunctate, broad, pollinose, its lateral wall a medially-directed scarp; pollinosity of parasutural stria continuing posteriorly, where it merges with that of intratubercular stria, and combined strip continues to midline along anterior slope of apical tubercle; Interval III convex, its apex forming short subapical tubercle which is scarcely dilated; tips of subapical tubercles separated by 3.5 times width of one of them; intratubercular stria impressed, pollinose, dilated; Interval IV broad, nearly flat, continuous with apical tubercle; latter moderately swollen; marginal stria complete, its base expanded, middle part (from basal 0.16 to middle) very fine, linear; apical part deeper, curving below apical tubercle; marginal stria entirely pollinose; submarginal stria impressed, ending opposite Sternum V of abdomen; sutural stria without setae (but apical impression without setae or with one or two setae in line with sutural stria); parasutural stria with complete series of seven to nine setae; intratubercular with two to four setae in apical 0.5; marginal stria with six to eight setae in apical 0.5; apical tubercle with three or four setae.

Metasternum with median sulcus; abdominal Sterna III-V each with dilated pollinose transverse sulci; that on Sternum III continuous; that of IV either continuous or very narrowly interrupted at midline; that of V distinctly but rather narrowly interrupted; female with large, deep lateral pit in Sternum IV; Sternum VI with short triangular transverse sulci broadly joined to greatly dilated marginal groove, partly isolating glabrous discal area (Fig. 21); tibial spurs of middle and hind legs decidedly unequal; male with anterior and posterior trochanters pointed; anterior femur of male with ventral side tuberculate; both calcaria are distinctly angulate proximally, separating basal transverse margin from oblique anterior margin, latter sloped to acute point; hind calcar larger than middle one.

This species is unique within the subgenus in having a setiferous puncture on the disc of the temporal lobe, in addition to the usual one in the orbital groove. Otherwise it is closest in form to *R. rimoganensis* (Miwa), but differs from the latter in having the median groove of the pronotum less dilated and in having the antennal lobe entirely pollinose.

Rhyzodiastes (Temoana) rimoganensis (Miwa 1934) NEW COMBINATION
(Fig. 18)

Clynidium (Rhyzodiastes) rimoganense Miwa 1934: 256-257 (note misspelling of generic name).
Rhyzodiastes rimoganensis (Miwa) Bell and Bell 1978.

Type Material.— HOLOTYPE, female. According to Miwa, from TAIWAN: Taihoku Province, Rimogan; coll. K. Obayashi, March 25, 1933. We have not studied the holotype, but have studied several specimens from Taiwan which agree closely with the original description and figure.

Description.— Length 5.5-6.9 mm. Antennal stylet short, conical, acute; tufts of minor setae on Segments V-X; basal setae present, though sparse on Segments VIII-X; Segment I pollinose dorsally; antennae otherwise without pollinosity; head slightly longer than wide; median lobe rather short, triangular, its apex acute, opposite middle of eye; antennal lobe glabrous, shining, well separated from median lobe; frontal space rather narrow anteriorly, becoming broad posteriorly; frontal grooves rather narrow, pollinose; temporal lobe 1.5 longer than wide; medial margins strongly curved, so that at middle, temporal lobes are separated by less than 0.5 of width of one of them; temporal lobe fringed with pilosity; orbital groove narrow but complete, angulate opposite posterior margin of eye; one temporal seta present, in orbital groove, posterior to eye; eye narrow, crescentic, about 0.75 of length of temporal lobe; genae glabrous, posterior face of temporal lobe pilose.

Pronotum moderately elongate, length/greatest width 1.57, widest at middle, sides distinctly, evenly curved; both base and apex distinctly narrowed; median groove moderately dilated, as broad as median pits; anterior median pit wider than posterior median pit, so margins of median groove slightly convergent posteriorly; posterior median groove displaced anteriorly, its anterior end at 0.20 of pronotal length anterior to pronotal base; median groove deep posterior to posterior median pit, but narrowed, its sides glabrous; median groove in and between median pits glabrous medially, but with lateral scarps pollinose; inner carina convex, its lateral margin sloping gradually into paramedian groove; paramedian groove bounded laterally by pollinose strip on vertical medial scarp of outer carina; medial margin of outer carina curved, slightly undulating; basal impression very small, narrowly closed posteriorly, connected to margin by strip of pollinosity; outer carina moderately narrow, tapered anteriorly; marginal groove fine, impressed, linear, complete; visible in dorsal view as is margin laterad to it; submarginal groove nearly complete, 0.95 of length of pronotum, becoming finely pollinose posteriorly; pronotal setae absent; notopleural suture not pollinose; sternopleural groove absent; pleural groove oblique; ventral surface of prothorax opalescent.

Elytra moderately elongate; elytral cauda absent; elytron with pilosity around scutellar pits, extending laterally to base of Interval II, but broadly interrupted in Interval III, and represented laterally only by small pilose area at base of marginal stria; sutural interval nearly flat; sutural stria impressed, faintly punctate, pollinose, finer than other striae, its apex slightly out-curved at apical 0.15 of elytron (in some specimens joining parasutural stria); Interval II nearly flat, sloped laterally; parasutural stria deep, its lateral wall a medially directed scarp, its extreme base curved medially, posterior its pollinosity combining with that of intratubercular stria, and the combined strip continuing across anterior face of apical tubercle to suture; Interval III nearly flat, its apex becoming slightly convex, forming subapical tubercle; latter scarcely dilated; subapical tubercles separated by 3.5 times width of one of them; intratubercular stria impressed, pollinose, dilated; Interval IV flat, continuous with apical tubercle; latter moderately swollen; marginal stria entire, impunctate, rather deep; submarginal stria impressed, ending opposite base of Sternum VI; sutural stria without setae; parasutural with two to seven setae; intratubercular stria with one seta near apex; marginal stria with several setae near apex; stria with two or three setae near apex; apical tubercle without setae.

Ventral surface of pterothorax and abdomen opalescent; metasternum not sulcate; male with flattened, microsculptured median area on abdominal Sterna I, II; abdominal Sterna III-V with pollinose transverse sulci, these entire on III, IV, narrowly interrupted at midline in V; female with lateral pits on Sternum IV; Sternum VI with triangular transverse sulci broadly joined to greatly dilated marginal groove, nearly isolating rhomboid glabrous area, latter in both sexes with pair of tubercles; tibial spurs of middle, hind legs unequal; male with front, hind trochanters pointed; anterior femur of male tuberculate ventrally; middle calcar small, pointed, acute; hind calcar small, obtuse. (Description of male characters taken from specimens from Nakanoshima.)

This species differs from *R. bipunctatus* in lacking a setiferous puncture in the middle of the temporal lobe and in having distinct submarginal groove of the pronotum. It differs from *R. mirabilis* and *R. convergens* in having basal setae on the antennae and more than one seta in the parasutural stria. The tubercles on Sternum VI are a unique but inconspicuous character of this species.

Distribution.— We have studied a female specimen from Taiwan: Puli (Hori), July 1954 "native collector" (BPBM). We tentatively assign to this species a series of 15 specimens from RYUKYU ISLANDS: Nakanoshima, Is. Tokara, 5 July, 1960, M. Sato leg. These do not appear to differ in form from the Taiwan specimen, except that the latter has seven setae in the parasutural stria, while the Nakanoshima specimens have two or three (or, unilaterally, one). However, we have not seen males from Taiwan, so it is possible that the populations from the two islands are not conspecific.

Rhyzodiastes (Temoana) mirabilis (Lea 1904) NEW COMBINATION
(Fig. 22)

Rhyzodes mirabilis Lea 1904: 80-81.

Rhyzodiastes mirabilis (Lea) Bell and Bell 1978.

Type Material.— According to the original description, from Cairns, Queensland, Australia. We have not studied it, but have studied an enlarged photograph of it, kindly sent by Barry Moore. It is a female.

Description.— Length 6.5-7.0 mm. Antennal stylet short, slightly flattened; tufts of minor setae present on Segments V-X; basal setae entirely absent from antenna; Segments I-X each with apical pollinose band; head as wide as long; median lobe triangular, pointed posteriorly, its apex opposite middle of eye; antennal lobe largely pollinose, but with small isolated frontal boss; frontal space rather narrow, its smallest diameter about 0.33 of width of temporal lobe; frontal grooves narrow, entirely glabrous; temporal lobe 1.8 longer than wide, medial margins strongly curved so that at middle temporal lobes are separated by about 0.33 times width of one of them; temporal lobe fringed with pilosity; orbital groove narrow, complete, sinuate posterior to eye; temporal seta present, on medial margin of orbital groove posterior to eye; eye narrowly crescentic, about 0.67 as long as temporal lobe; genae glabrous, posterior face of temporal lobe pilose.

Pronotum moderately elongate, length/greatest width 1.56; widest at middle, sides distinctly, evenly curved; base distinctly narrowed; apex less narrowed than base; median groove deep, narrowed between median pits, which are small; posterior median pit at basal 0.33 of length; groove posterior to posterior median pit as deep as remainder of groove, deepened at pronotal base to form a secondary posterior median pit; inner carinae together convex, sloping laterally into paramedian groove; paramedian groove bounded laterally by vertical pollinose scarp on medial margin of outer carina; medial margin of outer carina evenly curved; basal impression very small, triangular, its posterior margin pollinose (so impression appears open posteriorly); outer carina broad, 0.5 as wide as inner one bounded posteriorly by pollinosity which reaches hind angle and connects to marginal groove; marginal groove visible in lateral but not in dorsal view, rather broad, 0.33 as wide as outer carina, shallow, pollinose; submarginal groove absent; pronotal setae absent; sternopleural groove absent; pleural groove oblique; notopleural suture pollinose; prosternum with anterior margin narrowly pollinose, narrowly interrupted at midline.

Elytra moderately broad, without caudal lobe; each elytron with prominent parascutellar pit at base of sutural stria; these pits situated relatively far from one another, separated by glabrous area; elytron with complete transverse strip of pollinosity at base, not interrupted opposite Interval III; Interval I broad, flat; sutural stria straight, impressed, pollinose, its apex slightly recurved; Interval II nearly flat, sloped laterally; parascutellar stria impressed, straight, becoming slightly broader posteriorly, pollinose, its apex joined to intratubercular stria, and combined pollinosity continued posteriorly along anterior face of apical tubercle to suture; Interval III nearly flat, its apex convex, suddenly dilated, forming preapical tubercle; preapical tubercles separated by 3.5 times width of one of them; intratubercular stria impressed, pollinose; Interval IV flat, continuous with apical tubercle; latter scarcely dilated; marginal stria impressed, narrow, slightly dilated posteriorly, submarginal stria reaching base of Sternum V; sutural, parascutellar and intratubercular striae without setae; preapical tubercle with five or six setae; marginal stria with five to seven setae near apex.

Ventral surface not opalescent; metasternum not sulcate; abdominal sterna with pollinose transverse sulci which are interrupted at midline (broadly so except for Sternum III of female which is very narrowly interrupted); both sexes with rather small lateral pits on Sternum IV; Sternum VI with dilated submarginal groove which connects anteriorly to transverse sulci, nearly isolating rhomboid glabrous area; latter not tuberculate; spurs of middle and hind tibiae equal; male with anterior, posterior trochanters pointed; anterior femur of male tuberculate ventrally; middle and hind calcei with slight "shoulder" angle on dorsal margin, calcei triangular, their apices obtuse.

The rounded temporal lobes of this species suggest *R. rimoganensis*, but it differs from the latter species in lacking basal setae on the antennae, and lacks a submarginal groove on the pronotum. It also has the elytral setae much more restricted, and has a small, isolated glabrous spot on each antennal lobe. The shape of the pronotum, wider at apex than base, is distinctive and separates it from *R. indigenus*.

Distribution.— Restricted to Queensland. We have seen specimens from the following localities: one male, one female, Shipton's Flat (south of Cooktown), June, 1958, coll. Darlington (MCZ); one male, Upper Little Mulgrave, 3-VIII-69, coll. James Tobler (CAS); one female, labelled, "Queensl. Myoberg" (LUN); one male, one female, labelled "N. Queensland, Redlynch, 12-20-VIII-1938, R. G. Wind" (BMNH). The female of this pair is in all respects *R. mirabilis* except for a deep median pit in Sternum VI. Whether or not this is an anomaly will depend on the study of more specimens.

Rhyzodiastes (Temoana) indigens new species

(Fig. 23)

Type Material.— HOLOTYPE male, labelled: "SUMATRA, Si Rambé, XII-90-III-91, E. Modigliani", (GEN). PARATYPE one male, two females, same label as holotype (GEN). The female is labelled as a syntype of *R. gestroi*, but is not conspecific with it, and does not have convergent temporal lobes, as specified in the original description of the latter species.

Description.— Length 8.0-9.0 mm. Antennal stylet short, conical; tufts of minor setae on Segments V-X; Segments I-X each with subapical pollinose ring; basal setae of Segments IX, X one or two or absent; head slightly longer than wide; median lobe triangular, tip pointed, opposite anterior end of eye; frontal grooves rather wide, deep, glabrous; temporal lobe more than two times longer than wide; median margins curved, posteriorly oblique, slightly divergent; temporal lobe fringed posteriorly and on posterior 0.5 of medial margin with pilosity; orbital groove complete; one temporal seta in orbital groove posterior to eye; eye narrowly crescentic, about 0.67 of length of temporal lobe; genae glabrous, posterior face of temporal lobe pollinose.

Pronotum short, length/greatest width 1.37, widest near middle, sides curved; base moderately narrowed, apex very strongly narrowed, median groove deep, anterior 0.5 as wide as anterior median pit, constricted posterior to middle, then broadened to posterior median pit; groove posterior to posterior median pit as deep as at middle; inner carinae together convex, sloped laterally to paramedian groove; paramedian groove bounded laterally by vertical pollinose scarp on medial margin of outer carina; latter evenly curved; basal impression small, triangular, open posteriorly; outer carina broad, 0.5 as wide as inner one at middle, strongly narrowed anteriorly, extreme apex pollinose, marginal groove visible in dorsal view; submarginal groove absent; pronotal setae absent; sternopleural groove absent; pleural groove oblique, notopleural suture glabrous.

Elytron moderately broad, without caudal lobe; elytron with basal pollinosity interrupted at Interval III; Interval I broad, slightly convex, sutural stria straight, impressed, pollinose, apex slightly recurved; Interval II nearly flat, sloped laterally; parasutural stria impressed, straight, pollinose; apex joined to intratubercular stria; Interval III, raised above level of Interval II, nearly flat; preapical tubercle inflated; preapical tubercles separated by 1.5 width of one of them; intratubercular stria impressed, pollinose; Interval IV flat, continuous with apical tubercle; latter inflated; marginal stria impressed, not dilated posteriorly; submarginal stria reaching base of Sternum V; parasutural stria with one or two setae near apex; intratubercular stria with one seta near apex; marginal stria with four setae near apex.

Ventral surface not opalescent; metasternum not sulcate; abdominal sterna with transverse sulci broadly interrupted in midline in both sexes; each sulcus with prominent medial, lateral pit; female with large lateral pit on Sternum IV; Sternum VI with submarginal sulcus widely separated from transverse sulci; middle, hind tibiae with spurs nearly equal; male with anterior, posterior trochanters pointed; ventral surface of anterior femur of male with many small tubercles; tibiae thick; middle calcar triangular, small, acute; hind calcar larger, acute, dorsal margin convexly curved.

Among members of the *singularis* group, this species comes closest to *R. mirabilis*. It differs from the latter in having a much shorter pronotum which is strongly narrowed anteriorly. In appearance it comes close to *R. bonsae* in the *gestroi* group, but the latter species has the outer carina of the pronotum shallowly concave and the tufts of minor setae on the antenna beginning on Segment IV.

Rhyzodiastes (Temoana) convergens new species

(Figs. 24, 30)

Type Material.— HOLOTYPE male, labelled: "New Britain, Gisiluve, Nakanai Mts., 1050 m., July 26, 1956, coll. E. J. Ford, Jr." (BPBM). PARATYPES two males, two females, same data as holotype (BPBM); two males, one female, same data as holotype but dated July 25, 1956 (BPBM).

Description.— Length 6.2-7.2 mm. Antennal stylet short, acuminate; tufts of minor setae present on Segments V-X; basal setae of antennae entirely absent; head distinctly longer than wide; median lobe short, broad, at widest point 0.33 of width of head, its apex opposite anterior end of eye; parafrontal boss rather large, narrowly separated from antennal rim; frontal grooves rather broad, deep, pollinose; temporal lobe about two times longer than broad, medial margins shallowly emarginate, margins divergent posterior to median lobe; then convergent, shallowly sinuate to occipital angles; latter separated by about 0.20 of width of head; medial margin of temporal lobe with fringe of very fine pollinosity; posterior margin with fringe of pilosity; orbital groove not quite complete, ending posteriorly at temporal seta, not quite attaining basal pilosity; orbital groove barely sinuate posterior to eye; one temporal seta present, on orbital groove near to posterior margin of temporal lobe; eye narrowly crescentic in lateral view, 0.67 as long as temporal lobe; genae glabrous; posterior face of temporal lobe pilose.

Pronotum elongate, length/greatest width about 1.67; widest at middle, sides distinctly curved; both base and apex narrowed; median groove deep, narrow, parallel-sided, scarcely enlarged opposite median pits; posterior median pit at 0.16 of length; groove posterior to posterior median pit as deep as remainder of groove, but not forming distinct secondary posterior-median pit; inner carinae together convex, sloping laterally into paramedian grooves; paramedian grooves broad, bounded laterally by vertical pollinose scarp on medial margin of outer carina; medial margin of outer carina evenly curved; basal impression oblique, sloped up gradually to flat, very finely pollinose ridge which closes it posteriorly; outer carina broad, very convex, narrowed to both base and apex; pollinosity of median scarp connected to marginal groove at hind angle; marginal groove visible in lateral but not in dorsal view; marginal groove linear; submarginal groove absent; pleural groove oblique, impressed, rather narrow; notopleural suture pollinose; prosternum without pollinosity on anterior margin.

Elytra moderately broad, without caudal lobe; elytra with small, widely separated parascutellar pits at bases of sutural striae, with very little associated pilosity; basal pilosity of elytron narrowly interrupted opposite medial 0.5 of Interval III; Interval I broad, flat; sutural stria impressed, very finely pollinose, its apex curved laterally, to meet parascutellar stria; Interval II convex; parascutellar stria impressed, straight, becoming scarp-like posteriorly; Interval III nearly flat anteriorly, becoming convex posteriorly, forming scarp on lateral face near apex; subapical tubercle swollen, its median margin oblique, intratubercular stria impressed, linear anteriorly, becoming slightly dilated posteriorly, pollinose; Interval IV flat, connected to apical tubercle, latter impunctate, somewhat swollen; a pore ventrad to apical tubercles on suture; marginal stria fine, impressed, complete, pollinose; submarginal stria ends at apex of Sternum V; parascutellar stria with one seta posterior to middle; intratubercular stria with two setae in apical 0.2; marginal stria with three or four setae near apex.

Ventral surface not apalescent; metasternum with fine, incomplete medial sulcus limited to posterior 0.5; abdominal sterna with pollinose transverse sulci which are broadly interrupted medially in both sexes; both sexes with lateral pits on Sternum IV; Sternum VI with marginal groove connected anteriorly to transverse sulci, nearly isolating rhomboid glabrous area (Fig. 30); latter not tuberculate; spurs of middle, hind tibiae equal; male with anterior, posterior trochanters pointed; anterior femur of male neither dentate nor tuberculate ventrally; middle and hind calcaria "shouldered" on dorsal side.

This species resembles *R. mirabilis*, but is more elongate and narrow, with the pronotum more oval, and more narrowed at the apex. The medial sinuation on the temporal lobe is characteristic, but is very small in some specimens.

THE *MISHMICUS* GROUP

This contains the only species from west of Wallace's Line which have the tufts of minor hairs beginning on Antennal Segment V, except for *R. indigens*. The species resemble those of the *singularis* group except in having the orbital groove strongly abbreviated or absent and in lacking temporal setae. All species lack pronotal and elytral setae. The anterior pits are enlarged, rounded and conspicuous. The transverse sulci of the abdominal sterna are reduced. The group ranges from Thailand to extreme eastern India. *R. waterhousei* and *R. preorbitalis* appear more closely related to one another than to *R. mishmicus*. The latter species has a distinct though reduced orbital groove and a long median lobe, while the two former species have a preorbital pit rather than an orbital groove, and have a very short median lobe. On the other hand, *R. preorbitalis* lacks the distinct median metasternal sulcus found in the other two species. This suggests that the sulcus was acquired by the common ancestor of the group, and then secondarily lost in *R. preorbitalis*.

Rhyzodiastes (Temoana) mishmicus (Arrow 1942) NEW COMBINATION (Fig. 26)

Clinidium mishmicum Arrow 1942: 182-183.

Rhyzodiastes mishmicus (Arrow) Bell and Bell 1978.

Type Material.— HOLOTYPE male, labelled: ASSAM: "Mishmi Hills, Delai Valley, Chauiliang, i-xii, 1936, alt. 4840 ft.; (Miss) M. Steele BM 1937-324" (BMNH).

Description.— Length 7.0 mm. Antennal stylet prominent, acuminate; basal setae of antennae restricted to lateral surfaces, sparse, but present on Segments V-X; head as broad as long; median lobe triangular, long, its apex opposite posterior 0.5 of eye; frontal space very narrow, scarcely wider than one frontal groove; frontal grooves long, broad, deep, pollinose; length of temporal lobe 1.5 greater than its width; medial margin of temporal lobe evenly, convexly curved; inner

and posterior margins of temporal lobe broadly fringed with pilosity; orbital groove present, shallow, extending posteriorly to end even with middle of eye; eye short, crescentic, about 0.33 as long as temporal lobe.

Pronotum short, broad, length/greatest width 1.25; widest near middle, sides curved; apex strongly narrowed, base moderately so; median groove fine, linear; both median pits displaced towards middle of pronotum; anterior median pit in oval depression; median groove distinct but shallow posterior to posterior median groove; inner carina convex, glabrous, its lateral margin sloped gradually into paramedian groove; lateral margin of paramedian groove bounded by very narrow, inconspicuous strip of pollinosity on medial scarp of outer carina; outer carina broad, its width at middle about 0.67 of width of inner carina at same level; outer carina strongly tapered anteriorly, moderately so posteriorly; basal impressions deep but narrow, about 0.33 as wide as posterior part of inner carina; marginal groove narrow, distinct, visible in dorsal view; submarginal groove absent.

Elytra short, rather broad, their sides parallel; sutural interval pollinose at base; sutural stria fine, its apical fifth obsolete; parasutural stria complete, its base bent medially to reach base of sutural stria; intratubercular stria deeper than the others, complete; subapical tubercle somewhat elevated, its apex rounded; marginal stria fine, complete, impressed; apical tubercles small, contiguous, marginal stria with three setae below apical tubercle; elytral setae otherwise absent.

Metasternum with complete, deep, dilated median sulcus; male with triangular lateral pits on abdominal Sterna III-V, that of IV deeper than the other; pits not extended medially to form transverse sulci; Sternum VI with complete marginal groove; female unknown; middle and hind tibiae each with spurs equal; male with large, distally-directed ventral tooth on anterior femur and deep lateral groove on anterior femur; all trochanters rounded distally; calcars small; calcar of middle leg with apex level with bases of spurs; that of hind leg with apex raised well above level of spurs.

The presence of a short orbital groove, the short, broad form of the body, the fine median groove of the pronotum, and the elongate median lobe of the head easily distinguish this species from the other members of the group. *R. myopicus*, in the *myopicus* group, is superficially similar in appearance, but has the tufts of minor hairs beginning on Segment IV of the antennae, the orbital groove entirely absent, tibial spurs strongly unequal, and the abdominal sterna with prominent transverse sulci.

Rhyzodiastes (Temoana) waterhousei (Grouvelle 1910) NEW COMBINATION (Fig. 25)

Clinidium (Rhyzodiastes) waterhousei Grouvelle 1910: 326-327.

Rhyzodiastes waterhousei (Grouvelle) Bell and Bell 1978.

Type Material.— HOLOTYPE female, labelled: "BIRMAH: Ruby Mines (coll. Doherty) 64626 Fry Coll. 1905.100" (BMNH)

Description.— Length 6.5 mm. Antennal stylet prominent, conical; basal setae numerous on Segments VII-X; head as broad as long; median lobe triangular, short, its apex opposite anterior end of eye; anterior tentorial pits very large, separated by less than the width of one of them; frontal space parallel-sided, elongate, its width about 0.33 of width of one temporal lobe; frontal grooves narrow, shallow, temporal lobe 1.5 longer than wide; medial margin of temporal lobe almost straight, forming obtuse angle with posterior margin; posterior margin of temporal lobe broadly fringed with pollinosity, medial margin glabrous; orbital groove absent; preorbital pit present; eye narrowly crescentic, rather elongate, about 0.67 of length of temporal lobe.

Pronotum moderately long, length/greatest width about 1.36; widest near middle; base distinctly narrowed; apex strongly so; median groove narrow, sublinear, deeper than in *R. mishmicus*; both median pits displaced towards middle of pronotum; anterior median pit in oval depression; median groove distinct but shallow posterior to posterior median pit; inner carina convex, glabrous, its lateral margin sloped gradually into paramedian groove; basal impressions broad, deep, distinctly wider than posterior part of inner carina; the base of latter consequently distinctly narrower than in *R. mishmicus*; lateral margin of paramedian groove bounded by narrow strip of pollinosity on medial margin of outer carina; outer carina broad, its width near middle about 0.67 of width of inner carina at same level; outer carina distinctly narrowed anteriorly, and posteriorly; marginal groove narrow, complete, visible in dorsal view; a shallow submarginal groove present, visible only in lateral view.

Elytra rather short, the sides nearly parallel; sutural interval pollinose at base; sutural stria rather fine, complete, its apex joining parasutural; sutural stria obsoletely punctate; Interval II distinctly convex; parasutural stria impunctate, more deeply impressed than sutural stria, its base bent medially to reach base of sutural stria; Interval III distinctly convex; intratubercular stria slightly less impressed than parasutural; subapical tubercle somewhat elevated, its apex rounded; marginal stria impressed, fine, complete; apical tubercles small, contiguous; marginal stria with three or four setae below apical tubercle; elytral setae otherwise absent.

Metasternum with complete, deep, linear median sulcus; abdominal sterna with short transverse sulci which are dilated laterally and which have a small pit at medial end; transverse sulci separated medially by approximately 0.33 of width of sternum; female with deep lateral pit on Sternum IV; middle and hind tibiae each with spurs equal; anterior

femur of female not angulate; male unknown.

This species is most similar to *R. preorbitalis*, but the latter species lacks the median sulcus on the metasternum, has the anterior tentorial pits less enlarged, the transverse sulci of the abdomen more poorly developed, and the anterior femur of the female is strongly angulate ventrally. *Rhyzodiastes vadiceps*, in the *myopicus* group, is superficially similar to the two preceding species, but has the tufts of minor setae beginning on Antennal Segment IV, and the occiput largely glabrous and distinctly notched in lateral view.

Rhyzodiastes (Temoana) preorbitalis new species
(Figs. 29, 31)

Type Material.— HOLOTYPE female, labelled: "THAILAND: E. slope Doi Sutep, 875-950 m., 15-VII-1962, coll. E. S. Ross, D. O. Cavagnero" (CAS). PARATYPE one female, labelled: "Doi Sutep, Siam, Feb. 10, 1928, Coll. Alice Mackie" (NMNH).

Description.— Length 6.8-7.8 mm. Antennal stylet small, acute; basal setae numerous on Segments VII-X; head as broad as long; median lobe short, triangular, its apex entirely anterior to eye; anterior tentorial pits moderately large, separated by 1.5 times the width of one of them; frontal space parallel-sided, elongate, its width about 0.33 of width of one temporal lobe; frontal grooves narrow, shallow, glabrous, temporal lobe 1.5 times longer than wide; medial margin of temporal lobe almost straight, forming angle with posterior margin; posterior margin of temporal lobe rather narrowly fringed with pilosity; medial margin glabrous; orbital groove absent; preorbital pit present; eye narrow, crescentic, less than 0.5 of length of temporal lobe.

Pronotum rather elongate, length/greatest width about 1.42; widest near middle, sides curved; base moderately narrowed; apex very strongly narrowed; median groove fine, linear, both median pits displaced towards middle of pronotum; anterior median pit in long, oval depression; median groove represented by fine, shallow line posterior to posterior median pit; inner carina convex, glabrous, sloped gradually to paramedian groove; basal impressions broad, deep, distinctly wider than posterior part of inner carina; the base of latter narrowed as in *R. waterhousei*; lateral margin of paramedian groove bounded by narrow strip of pollinosity on medial margin of outer carina; outer carina rather broad, its width at middle about 0.50 of width of inner carina at same level; outer carina distinctly narrowed anteriorly and posteriorly; marginal groove fine, complete, visible in dorsal view; submarginal groove short, oblique, restricted to basal 0.20 of pronotum, visible only in lateral view.

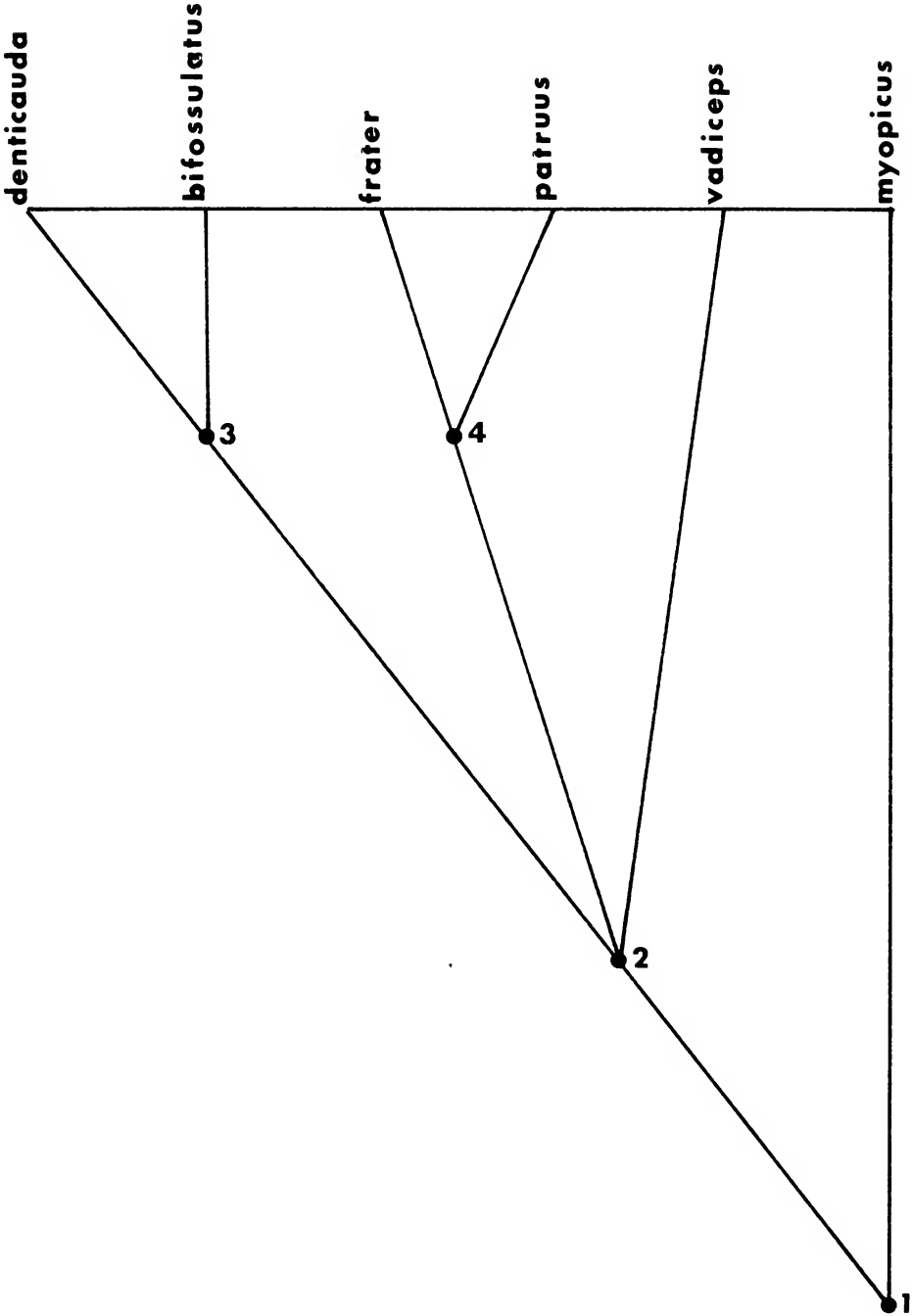
Elytra rather short, their sides nearly parallel; sutural interval pollinose at base; sutural stria rather fine, complete, impunctate; Interval II slightly convex; parasutural stria impunctate, more deeply impressed than sutural stria, its apex bent medially to reach base of sutural stria; Interval III distinctly convex; intratubercular stria complete, slightly less impressed than parasutural; subapical tubercle somewhat elevated, its apex rounded; marginal stria fine, scarcely impressed at middle, becoming finely punctate and more distinctly impressed posteriorly, where it passes below apical tubercle; apical tubercles small, contiguous; apex of marginal stria with three or four setae below apical tubercle; elytral setae otherwise absent.

Metasternum with elongate median impression near posterior margin, but without median sulcus; abdominal sterna with transverse sulci scarcely developed, each appearing as short medial extension from triangular lateral pit in Sterna III, IV, V; female with lateral pits of IV deeper than the others (Fig. 31); middle and hind tibiae each with two equal spurs; anterior femur of female strongly angulate ventrally; male unknown.

This species is closest to *R. waterhousei*, but differs sharply in lacking a median sulcus on the metasternum, in having the anterior tentorial pits less enlarged, and in having the anterior femur of the female strongly angulate ventrally.

THE MYOPICUS GROUP

The members of this group have the tufts of minor setae beginning on Segment IV of the antenna, and the median groove of the pronotum linear. Some species, particularly *R. myopicus*, resemble the *mishimicus* group in having a short, broad head, with the orbital groove absent or very reduced. In others the head is elongate, and the orbital groove more distinct. All species differ from the *mishimicus* group in having strongly developed transverse sulci on the abdominal sterna, and in having a tuft of minor setae on antennal Segment IV. The *gestroi* and *fairmairei* groups resemble the *myopicus* in the latter respect, but differ in having the median



Phylogenetic Diagram 1. Reconstructed Phylogeny of species of *Rhyzodiastes* subgenus *Temoana*, *Myopicus* group.

groove of the pronotum dilated. Many of them have numerous elytral setae, while the *myopicus* group lack such setae, except, in some species, near the apex of the marginal stria.

There are six species, two from the Malay Peninsula, three from Borneo, and one of unknown range, but probably also from Borneo.

Phylogeny.— A possible phylogeny for the group is illustrated in Diagram 1. Species 1, the hypothetical ancestor for the group, probably had the following characters: antennal stylet long; Segment XI elongate, nearly cylindrical; basal setae present; antennal segments not thickened; orbital groove, one temporal seta present; base of parasutural stria straight; preapical tubercle not elevated; apical tubercles thickened, contiguous, elytral humeri not narrowed; setae present in apex of marginal stria; tibiae slender; at least anterior femur of male with many tubercles on ventral surface; middle, hind tibial spurs equal; male trochanters rounded at apex.

R. myopicus appears to be the sister species to Species 2, the hypothetical ancestor of the five remaining species. Apomorphic features of *R. myopicus* include loss of the orbital groove, the short, very flat head with strongly reduced eyes, and the strongly unequal tibial spurs. Probable plesiomorphic features include base of parasutural stria straight; antennae and tibiae slender; one temporal seta retained; setae in apex of marginal stria retained; elytral humeri not narrowed; antennal Segment XI cylindrical; trochanters of male rounded. The broad anterior truncation of the pronotum and outer carina are of uncertain significance.

Species 2 probably had the following apomorphic features: base of parasutural stria bent sharply medially at base; humeral region of elytra strongly narrowed; antennae, tibiae strongly thickened; antennal Segment XI compressed, short; at least hind trochanter of male pointed. Like *R. myopicus* it probably retained a temporal seta and several subapical setae in the marginal striae, although these have been lost in some of its descendants. Unlike *R. myopicus* it had the pronotum narrowed anteriorly, with the outer carina not truncate at the apex.

We postulate three species descended from Species 2. Species 3, Species 4, and *R. vadiceps*. Species 3 showed the following specializations: outer antennal segments with complete pollinose rings; preapical tubercle elevated, tooth-like; apical tubercle bounded anteriorly by deep transverse notch; basal setae of antennae entirely absent. Unspecialized features retained from Species 2 included equal tibial spurs; one temporal seta; one seta in apex of marginal stria; marginal groove present on pronotum, though shallow; male with trochanters 1 and 3 pointed; and femora 1 and 3 tuberculate ventrally.

Species 4 showed striking specializations in the apex of the middle and hind tibiae; only one tibial spur is present, while there is a curved apicolateral process. Other apomorphic characters included loss of setae of the marginal stria. Possible plesiomorphic characters include retention of basal setae on the antennae and of the marginal groove of the pronotum.

R. vadiceps shows the complete loss of the marginal groove of the pronotum as a specialization. Possibly the elongate antennal stylet is also an apomorphic feature, as are loss of marginal and temporal setae. Most of its other characters are plesiomorphic, for instance, the retention of two equal tibial spurs. The antennal segments are less thickened than in the descendants of Species 3 and 4. Of uncertain significance are the secondary sexual characters of the male. This species and *R. patruus* are the only species in which all three pairs of femora are tuberculate ventrally. If all were tuberculate in the male of Species 2, then the absence on some legs in the remaining species can be interpreted as a secondary loss. Likewise, the loss of the point on the anterior trochanter in *R. vadiceps* is probably secondary, as both anterior and posterior trochanters are pointed in the remaining descendants of Species 2, with the possible exception of *R. denticauda*, of which the male has not been collected.

Species 3 gave rise to *R. bifossulatus* and *R. denticauda*. *R. bifossulatus* is specialized by the great elevation of the preapical tubercles, which are close together. Otherwise, it is probably much like Species 3. It is the only member of the group besides *R. vadiceps* to retain setae in the marginal stria, and shares with the latter species and *R. patruus* the retention of the temporal seta. *R. denticauda* shows a unique specialization on the separation of the prominent, subtruncate apical tubercles. It has also lost both temporal and elytral setae. The preapical tubercles are less specialized than are those of *R. bifossulatus*, being further apart and somewhat less elevated. Unfortunately the secondary sexual characters of the male are unknown.

Species 4 gave rise to *R. frater* and *R. patruus*. *R. frater* has lost the temporal seta and the ventral tubercles on the femora. A plesiomorphic feature is the retention of the basal setae of the antenna. *R. patruus* has lost the basal setae. The tubercles and the projecting angle on the hind tibia of the male are clearly apomorphic features, while the retention of ventral tubercles on all femora of the male and the retention of a temporal seta are clearly plesiomorphic.

Rhyzodiastes (*Temoana*) *myopicus* (Arrow 1942) NEW COMBINATION
(Figs. 27, 32)

Clinidium myopicum Arrow 1942: 182.

Rhyzodiastes myopicus (Arrow) Bell and Bell 1978.

Type Material.— LECTOTYPE male, labelled: "FEDERATED MALAY STATES: Pahang, Cameron's Highlands, Bukit-Lendong, 5000 ft., May 21, 1931, coll. H. M. Pendlebury" (BMNH). PARATYPE According to Arrow there was a second specimen, sex unstated, collected with the type. We have been unable to locate it. If it still exists, it is a paralectotype.

Description.— Length 6.3-7.5 mm. Antennal stylet short, conical; antennal Segment XI longer than broad; sparse basal setae on Segments IX, X; antennal pollinosity restricted to Segment I; head as broad as long, strongly flattened; antennal lobe pollinose; median lobe somewhat cross-shaped with lateral lobe posterior to each tentorial pit; tip of median lobe acute, posterior to middle of eye; frontal grooves very narrow, shallow, postantennal pit scarcely evident; medial margin of temporal lobe curved; temporal lobe less than 1.5 longer than wide posterior margin; posterior 0.5 of medial margin narrowly fringed with pilosity; orbital groove entirely absent, eye narrow, short, less than 0.33 of length of temporal lobe; one temporal seta, near posteriormost point on temporal lobe; postorbit, genal lobe pilose.

Pronotum moderately elongate, length/greatest width 1.40; basal margin strongly curved; lateral margins rather weakly curved; base, apex moderately narrowed; apex truncate, with distinct anterior angles; median groove fine, linear; median pits narrow, not displaced from base, apex; inner carinae glabrous, together forming convex discal area, sloped gradually into paramedian grooves; medial margin of outer carina with narrow pollinose strip; basal impression small, oblique; outer carina broad, its width near middle about 0.5 of width on inner carina at same level; outer carina slightly curved, of nearly even width, anterior end truncate; marginal groove impressed, complete, clearly visible in dorsal view; submarginal groove represented by impression in basal 0.12 of pronotum; pronotal setae absent.

Elytra with sides parallel, base scarcely narrowed; sutural stria deep, entire, obsoletely punctate; Interval II less depressed than Interval I; parasutural stria impressed, impunctate, base straight; Interval III slightly convex, apex (subapical tubercle) not swollen; intratubercular stria complete, impressed, impunctate; marginal stria fine, complete, impressed; apical tubercles slightly swollen, contiguous at suture, with minute pore ventral to them in midline; marginal stria with three to six setae below apical tubercle; elytral setae otherwise absent.

Metasternum without median sulcus; abdominal Sterna III-V with prominent transverse sulci; in male, III, IV continuous across midline, V narrowly interrupted at midline; in female all sulci narrowly interrupted medially (Fig. 32); both sexes with enlarged lateral pit on Sternum IV; Sternum VI with transverse sulci at base, curved submarginal sulcus; abdominal sulci narrow; middle, hind tibiae rather slender, with inner spur shorter than outer one; anterior femur of male tuberculate ventrally, with small ventral tooth; all trochanters of male rounded distally; both pairs of calcaria small, acutely pointed.

The broad pronotum, broad outer carinae with anterior end truncate and the flat head and small eyes are distinctive of this species. The most similar member of the *myopicus* group is *R. frater* of Borneo. The latter species is much longer and more slender, has the outer carina of the pronotum narrower, and lacks the temporal seta. *R. mishmicus*, of the *mishmicus* group, is also rather similar in appearance but lacks a tuft of minor setae on antennal Segment IV, lacks the

transverse sulci on the abdominal sterna, and has the spurs of each middle and hind tibia equal.

R. patruus is the only other member of the species group from the Malay peninsula. It differs from the present species in having the outer carina very narrow, the head narrow and elongate, and in having only one tibial spur and an apicolateral process.

Range.— *R. myopicus* is known only from the Malay Peninsula. In addition to the lectotype, we have seen the following specimens: one male, labelled: "Malaya, G. Batu, Brinchang, 6500', VI-19-62, coll. E. S. Ross & D. Cavagnaro" (CAS); two females, labelled: "Malaya, Pahang, Cameron Highlands, Mt. Brinchang, coll. L. W. Quate" (BPBM). One is dated, 1-4-1959, 1980 m., the other 5-1-1959 at 1900 m. "in dead wood".

Rhyzodiastes (Temoana) vadiceps new species
(Figs. 28, 33)

Type Material.— HOLOTYPE male, labelled: "Mjoberg Coll., W. W. Funge Bequest" (CAS). No locality is given. Borneo is a likely if unproven provenance, firstly because the closest relatives of the species, *R. frater*, *R. bifossulatus*, and *R. denticauda* are all from Borneo, and secondly, because Mjoberg is known to have collected in Borneo. The type specimens of *Omoglymmius fraudulentus* Bell and Bell and *Rhyzodiastes denticauda*, described herein, both have labels identical to that on the type of *R. vadiceps*, in addition to labels for specific localities in Borneo. If not from Borneo, this species might be from one of the Greater Sunda Islands or possibly from the Malay Peninsula.

Description.— Length 8.5 mm. Antennal stylet acute, longer than in other members of group; antennal Segment XI slightly compressed; slightly longer than wide; outer antennal segments strongly thickened, oblate sphaeroidal; tufts of minor setae present on Segments IV-X; basal setae entirely absent; antennal pollinosity restricted to Segments I, II; head 1.5 longer than wide antennal lobe glabrous; median lobe triangular, tip acute, opposite anterior 0.33 of eye; frontal grooves shallow, glabrous; postantennal pit small; lateral margin of frontal groove sloped gradually to temporal lobe; medial margin of temporal lobe long, oblique, sinuate near occipital angle; temporal lobe 2.5 longer than wide; margin lined with short pollinosity near occipital angle; orbital groove represented by very minute pollinosity medial to eye, invisible except under high magnification; small preorbital pit present; eye short, about 0.5 of length of temporal lobe, broader than in *R. myopicus*; temporal setae absent; genal lobe prominent, rectangular, nearly glabrous, separated from temporal lobe by deep, pollinose notch.

Pronotum elongate, length/greatest width 1.60; basal margin transverse; lateral margins strongly curved; base, apex strongly narrowed; anterior angles indistinct; median groove fine, linear; median pits large, oval, not displaced from base, apex; inner carinae glabrous, together forming convex disc, sloped gradually to paramedian grooves; medial margin of outer carina with only a trace of pollinosity; basal impressions small; outer carina tapered anteriorly, widest at middle; marginal groove entirely absent; submarginal groove absent; pronotal setae absent.

Elytra with sides parallel near middle; base strongly narrowed; sutural stria deep, its apex effaced, obsoletely punctate; parasutural stria complete, impressed, more so apically, faintly punctate, base bent medially nearly to base of sutural stria; Interval III convex, its apex elevated, forming distinct preapical tubercle; intratubercular stria fine, complete; apical tubercles swollen, contiguous at midline, meeting medially above slit-like pore; elytral setae entirely absent.

Metasternum without median sulcus; midline of abdomen elevated, slightly cariniform, separating dilated transverse sulci; Sternum VI with transverse sulci, also with dilated submarginal sulcus; shallow lateral pit present on Sternum IV in male (Fig. 33); tibiae moderately thick; spurs equal; male with ventral surface of all femora with many minute tubercles; front, middle trochanters of male rounded at apex hind trochanter acutely pointed; middle, hind calcei large, acutely pointed, proximal margin strongly angulate; female unknown.

This species is closest to *R. frater*, from which it differs most conspicuously in the absence of the marginal grooves of the pronotum, in the very shallow frontal grooves with indistinct lateral margins, and in the great reduction of the pollinosity of the postorbital region and of the genal tubercles.

Rhyzodiastes (Temoana) frater (Grouvelle 1903) NEW COMBINATION
(Figs. 34, 40, 42)

Clinidium frater Grouvelle 1903: 135-136.

Rhyzodiastes frater (Grouvelle) Bell and Bell 1978.

Type Material.— HOLOTYPE male, labelled: "Born. Occ., Riv. Sambay, près Ngabang, J. B. Ledru 1887" (MNHN). This locality is in the northwestern part of Indonesian Borneo.

Description.— Length 5.9–8.0 mm. Antennal stylet minute, conical; antennal Segment XI compressed, as wide as long; outer antennal segments very short, thick, cylindrical, disc-like; tufts of minor setae present on Segments IV–X; basal setae present, though sparse on Segments III–X; Segments I–III with subapical pollinose rings; pollinosity of outer segments restricted to areas close to bases of setae; Segment I with prominent swellings around base of two setae of anterior aspect.

Head 1.5 times longer than wide; antennal lobe glabrous; median lobe hastate, short, narrow, tip acute, just posterior to anterior margin of eye; frontal grooves glabrous, moderately deep, margins distinct; tentorial, postantennal pits large; medial margin of temporal lobe long, oblique; temporal lobe 3.0 longer than wide; posterior margin and posterior 0.33 of medial margin fringed with long pilosity; orbital groove very fine, shallow, pollinose, in a few specimens interrupted posterior to eye; eye narrow, crescentic, 0.67 as long as temporal lobe; temporal setae absent; genal lobe, lower surface of temporal lobe long pilose, partly concealing notch between them.

Pronotum elongate; length/greatest width 1.54; widest behind middle; basal margin slightly oblique on either side of midline, where obtusely angulate; lateral margins curved; apex strongly narrowed; median groove fine, linear; median pits large, oval, not displaced from base, apex; inner carina glabrous, together forming convex discal area, sloped gradually to paramedian groove; medial margin of outer carina with narrow strip of pollinosity; basal impressions small, oblique; outer carina widest posterior to middle, tapered anteriorly; lateral part of outer carina shallowly concave; marginal groove fine, linear, ventrad to concavity of outer carina; submarginal groove, pronotal setae absent.

Elytra elongate, lateral margins parallel near middle, obliquely narrowed to humerus; swollen apical tubercles form large but ill-defined cauda; sutural stria nearly complete, impressed, minutely punctate, apex effaced; parasutural stria complete, impressed, base bent medially nearly to base of sutural stria; Interval III convex, apex elevated, forming distinct preapical tubercle; intratubercular stria fine, complete; marginal stria effaced near humerus, otherwise narrow, complete to suture; apical tubercles swollen, contiguous at midline, meeting medially above round pore (Fig. 42); elytral setae entirely absent.

Metasternum with fine trace of median sulcus in posterior 0.5; mid-line of abdomen elevated, cariniform, separating dilated transverse sulci; transverse sutures of abdomen deeply impressed; Sternum VI in both sexes with transverse sulci, also broad, deep subapical depression occupying 0.67 of sternum, bounded posteriolaterally by impressed marginal groove; in both sexes, Sternum IV with rather small lateral pit; tibiae thick; middle and hind tibiae each with one spur, also with acute, medially-curved apicolateral process (Fig. 40); ventral surface of femur in male smooth, not tuberculate; front, hind trochanters of male acutely pointed; middle, hind calcars large, acutely pointed, proximal margin angulate.

This species is closest to *R. patruus* of the Malay Peninsula, which it resembles in having only one spur and an apicolateral process on the middle and hind tibiae. *R. frater* differs from the latter species in lacking a temporal seta, in having basal antennal setae, in having the intratubercular stria impressed, and in lacking tubercles on the femora of the male.

It differs from the two remaining Bornean species, *R. denticauda* and *R. bifossulatus* in not having the apical tubercle separated from the outer intervals by a notch, and in having the preapical tubercle less elevated and less tooth-like.

Range.— Northwestern Borneo, including both the Indonesian Borneo and Sarawak. In addition to the holotype we have studied a series of 13 males, three females labelled: "Mt. Matang, W. Sarawak, G. E. Bryant, Bryant Colln., 1919–147" with various dates from XII-1913 to II-1914 (BMNH).

Rhyzodiastes (Temoana) patruus new species

(Figs. 35, 41, 43)

Type Material.— HOLOTYPE male, labelled: "Malaisie Johor, Sedili Kechil, 15-VIII-72. T. Jaccoud" (GVA).

Description.— Length 5.3 mm. Antennal stylet minute, conical; Segment XI slightly compressed, as wide as long; outer antennal segments very short, thick, cylindrical, disc-like; tufts of minor setae present on Segments IV–X; basal setae entirely absent; Segments I–X with complete subapical pollinose rings; Segment I with carina on dorsal surface.

Head 1.5 longer than wide; antennal lobe glabrous; median lobe hastate, short, narrow, tip acute, just posterior to anterior margin of eye; frontal grooves glabrous, moderately deep, margins distinct; tentorial, postantennal pits large; medial margin of temporal lobe long, oblique; temporal lobe 3.0 longer than wide, posterior margin, posterior 0.33 of medial margin fringed with pollinosity; orbital groove very fine, pollinose, complete; eye narrow, crescentic, 0.67 as long as temporal lobe; lateral margin of temporal lobe posterior to eye more oblique than in *R. frater*; temporal seta present; genal lobe, lower surface of temporal lobe long, pilose, partly concealing notch between them.

Pronotum elongate; length/greatest width 1.58; widest behind middle; basal margin slightly oblique on either side of midline, but not angulate at midline; lateral margins curved; apex strongly narrowed; median groove fine, linear; median pits large, oval, not displaced from base, apex; inner carinae glabrous, together forming convex discal area, sloped gradually to paramedian groove; medial margin of outer carina with narrow strip of pollinosity; basal impression small;

outer carina widest posterior to middle, tapered anteriorly; lateral part of outer carina shallowly concave; marginal groove fine, linear, ventrad to concavity of outer carina; submarginal groove of outer carina absent.

Elytra elongate; lateral margins parallel near middle, obliquely narrowed to humerus; apical tubercles less swollen than in *R. frater*; sutural stria complete, impressed, minutely punctate; parasutural stria complete, impressed, base bent medially nearly to base of sutural stria; Interval III convex, apex elevated, forming distinct preapical tubercle (Fig. 43); intratubercular stria impressed, pollinose near apex, otherwise effaced, marked only by elevated medial border of Interval IV; apical tubercles contiguous at midline, meeting above minute pore; setae of elytral striae entirely absent.

Metasternum without median sulcus; midline of abdomen less distinctly elevated than in *R. frater*; transverse sutures of abdomen deeply impressed; Sternum VI in male with transverse sulci, narrow subapical depression; tibiae thickened; middle, hind tibiae each with one spur, also with acute, medially curved apicolateral process; ventral surfaces of all femora of male tuberculate, anterior femur extensively so, middle femur with a few tubercles, hind one more densely tuberculate; trochanters of front, hind leg acutely pointed; calcaria acutely pointed; medial surface of hind tibia concave between calcar and basal angle, latter prominent, truncate; medial surface with two minute tubercles on either side of middle of length (Fig. 41); female unknown.

This species is closest to *R. frater* which it resembles in the presence of one tibial spur and a conspicuous apicolateral process on the middle and hind tibia. It differs from the latter in the presence of a temporal seta, absence of basal antennal setae, unimpressed intratubercular stria, and in having tuberculate ventral surfaces on the femora of the male.

Rhyzodiastes (Temoana) bifossulatus (Grouvelle 1903) NEW COMBINATION
(Figs. 36, 44)

Clinidium bifossulatum Grouvelle 1903: 139-140.

Rhyzodiastes bifossulatus (Grouvelle) Bell and Bell 1978.

Type Material.— HOLOTYPE male, labelled: "Borneo, Oberthuer Coll." (MNHN).

Description.— Length 6.7-8.0 mm. Antennal stylet conical, short; antennal Segment XI compressed, as wide as long; outer antennal segments very short, thick, cylindrical, disc-like; basal setae absent; Segments I-X each with subapical pollinose ring; latter interrupted ventrally on Segments IV-X by tuft of minor setae; Segment I with swellings around bases of two prominent setae on anterior aspect.

Head as wide as long; antennal lobe glabrous; median lobe very short, its tip acute, opposite anterior margin of eye; frontal grooves glabrous, moderately deep; frontal space very wide; tentorial, postantennal pits very large; antennal groove oblique, slightly dilated; temporal lobes 2.5 longer than wide; closest together opposite middle of eye, posterior 0.67 oblique, divergent; posterior margin of temporal lobe fringed with long pilosity; orbital groove complete, fine, pollinose, reaching posterior margin of temporal lobe; eye narrow, crescentic, 0.67 as long as temporal lobe; one temporal seta, in orbital groove posterior to eye; posterior margin of temporal lobe, postorbit long, pilose, concealing cleft between temporal, genal lobes; latter smaller, or shortly pilose than in *R. denticauda*.

Pronotum elongate; length/greatest width 1.57; widest behind middle; basal margin curved; lateral margins curved; apex strongly narrowed; base moderately so; median groove fine, linear; anterior median pit oval, elongate; posterior median pit round, separated from base by 0.2 of length of pronotum; inner carinae glabrous, together forming convex discal area, sloped gradually to paramedian groove; medial margin of outer carina with narrow strip of pollinosity; basal impressions small, deep, oblique; outer carina narrow, curved, bounded laterally by shallow broad concavity; ventral margin of latter with trace of minute pollinosity; posterior end of outer carina with tuft of pilosity; submarginal groove, pronotal setae absent.

Elytra elongate, lateral margins parallel near middle, obliquely narrowed to humerus; humerus with small lobe; apical lobes form prominent, narrow cauda; sutural stria impressed, faintly punctate, apex joining parasutural; parasutural stria complete, impressed, base bent medially to base of sutural stria; Interval III narrow, cariniform for most of length, base forming prominent, fringed medial angle; elevated preapical tubercle prominent; preapical tubercles closer together than in related species, separated by 0.5 of combined width of sutural intervals (Fig. 44); in lateral view, preapical tubercle with posterior margin emarginate; intratubercular stria shallow, broad; becoming obsolete ventrad to preapical tubercle; marginal stria impressed, connected by deep, narrow, glabrous impression to preapical impression, isolating apical tubercle from remainder of Interval III; portion of marginal stria beyond impression bent ventrally, passing across lower surface of apical tubercle to suture; apical tubercles swollen, contiguous at midline, meeting medially above slit-like pore; apex of marginal stria with one seta.

Metasternum with fine median sulcus in posterior 0.5; mid-line of abdomen scarcely carinate; abdominal sterna with deep, wide transverse sulci, scarcely interrupted in midline, interruption very narrow, pollinose; abdominal sutures deeply impressed; Sternum VI with transverse sulci, also deep marginal groove, delimiting central tubercle; small lateral pit on Sternum IV in both sexes; tibiae thick, coarsely punctate, each puncture with prominent seta; middle, hind tibiae each with two spurs; those of hind tibia equal; those of middle tibia very unequal, posterior spur minute, anterior one large, curved anteriorly; no apicolateral process; male with ventral surface of anterior, posterior femora with many small tubercles; male

with anterior, posterior trochanters pointed; middle calcar acute, hind calcar smaller than middle one, triangular; proximal margins of calcars not angulate.

This species and *R. denticauda* are characterized by having the preapical tubercle elevated and tooth-like, separated by a notch from the apical tubercle. In this species, the apical tubercles are contiguous at the suture, while in *R. denticauda*, they are separated.

Range.— Borneo, possibly restricted to the northeastern part. We have seen the following specimens with specific locality data, both from Sabah (The former British North Borneo): one male, labelled: "Sandakan, B. N. Borneo, Baker" (NMNH); one female labelled: "British North Borneo, Tawau, Quoin Hill, Cocoa Res. Sta., 30-VI-1962, Y. Hirashima, coll." (BPBM).

Rhyzodiastes (Temoana) denticauda new species

(Figs. 37, 45)

Type Material.— HOLOTYPE female, labelled: "Mt. Murud, Borneo, Mjöberg Coll., W. W. Funge Bequest" (CAS). This locality is in eastern Sarawak. PARATYPE one female, labelled: "SARAWAK: Claudetown, 25, vii, 1932, primitive white sand forest; Oxford Univ. Exp., B. M. Hobby and A. W. Moore, B.M.-1933-254" (BMNH). This locality is now called Marudi and is in eastern Sarawak, not far from Mt. Murud.

Description.— Length 6.8-7.0 mm. Antennal stylet conical, short; antennal Segment XI compressed, as wide as long; outer antennal segments very short, thick, cylindrical, disc-like; basal setae absent; Segments I-X each with subapical pollinose ring; latter interrupted ventrally on Segments IV-X by tuft of minor setae; Segment I swollen near bases of two prominent setae on anterior aspect.

Head 1.5 longer than wide; antennal lobe glabrous; median lobe short, hastate, tip acute, even with anterior margin of eye; frontal grooves glabrous, moderately deep; tentorial, postantennal pits very large; antennal groove transverse, very fine, its lateral 0.5 effaced; temporal lobe three times longer than wide, closest together opposite middle eye; posterior 0.67 oblique, divergent; posterior margin, posterior 0.33 of medial margin of temporal lobe fringed with pilosity; orbital groove very fine, complete, pollinose, reaching posterior margin of temporal lobe; eye relatively short, less than 0.5 of length of temporal lobe, narrow, crescentic; lateral margin of temporal lobe oblique posterior to eye; temporal setae absent; postorbit long, pilose, concealing notch between temporal, genal lobes; dorsal surface with conspicuous, reticulate microsculpture.

Pronotum very elongate; length/greatest width 1.67; widest behind middle; basal margin curved; lateral margins curved, convergent anteriorly; apex strongly narrowed; base moderately narrowed; median groove fine, linear; median pits oval, elongate; posterior median pit separated from base of pronotum by 0.2 of length of pronotum; inner carinae glabrous, together forming convex discal area; sloped gradually to paramedian grooves; medial margin of outer carina with narrow strip of pollinosity; basal impression small, transverse, oval; outer carina narrow, curved, bounded laterally by shallow broad concavity; ventral margin of latter with trace of minute pollinosity; posterior end of outer carina with tuft of pollinosity; submarginal groove, pronotal setae absent.

Elytra elongate, lateral margins parallel near middle, obliquely narrowed to humerus; latter with prominent lobe bounded posteriorly by pilose notch; apical lobes form prominent, narrow cauda; sutural stria scarcely impressed, faintly punctate; parasutural stria shallowly impressed, complete; base bent medially to base of sutural stria; Interval III narrow, cariniform for most of its length; base forming prominent, fringed medial angle; apex of Interval III forming prominent, elevated preapical tubercle; preapical tubercles separated by combined width of sutural intervals; in lateral view, preapical tubercle with posterior margin emarginate; intratubercular stria shallow, broad, becoming obsolete ventrad to preapical tubercle; marginal stria broad, shallowly impressed, connected by deep, semicircular notch to preapical impression, isolating apical tubercle from remainder of Interval IV; portion of marginal stria posterior to notch bent ventrally, passing across lower surface of apical tubercle; apical tubercles swollen, subtruncate medially, separated by about 0.5 of distance between preapical tubercles (Fig. 45); elytron entirely without setae.

Metasternum with fine median sulcus in posterior 0.5; midline of abdomen elevated, cariniform separating broad, deep transverse sulci; abdominal sutures deeply impressed; Sternum VI with transverse sulci at base, apex deeply impressed, impression bounded posteriorly by pollinose submarginal groove; female with deep lateral pit on Sternum IV; tibiae thick; middle, hind tibiae each with two small, equal spurs; apicolateral process absent. Male unknown.

This species is easily recognized by the separated apical tubercles of the elytra. These, together with the subapical tubercles, form four tooth-like elevations bounding the deep preapical impression.

THE *GESTROI* GROUP

This group consists of three species, two from Sumatra and one from the Nicobar Islands. They resemble the members of the *myopicum* group in most respects, but have the median groove of the pronotum narrowly dilated, with its sides pollinose and its floor glabrous. In contrast to the *fairmairei* group, the median groove is narrower than the median pits. The elytral setae are more extensive than in the *myopicum* group, with at least one seta in the intratubercular stria.

Phylogeny.— *R. bonsae* and *R. propinquus* are clearly closely related. They share the following characters: outer carina of pronotum concave dorsad to marginal groove; parasutural stria with many setae; median groove shallow, its margins glabrous posterior to posterior median pit; antennae short, thick, outer segments short, cylindrical, disc-like; Segment XI as wide as long, compressed, stylet short, conical; preapical tubercle strongly elevated; antennal lobe glabrous; temporal lobes divergent posteriorly.

The third species, *R. gestroi*, is more distantly related, and has the following contrasting characters: carina of pronotum convex; parasutural stria without setae; median groove basad to posteriormedian pit deep, its margins pollinose; antennae longer, more slender, outer segments oblate sphaeroidal; Segment XI longer than wide, not compressed; stylet longer, acute; preapical tubercle scarcely elevated; antennal lobe largely pollinose; temporal lobes strongly convergent posteriorly.

Rhyzodiastes (Temoana) gestroi (Grouvelle 1903) NEW COMBINATION
(Fig. 38)

Clinidium gestroi Grouvelle 1903: 136-137.

Rhyzodiastes gestroi (Grouvelle) Bell and Bell 1978.

Type Material.— LECTOTYPE (here designated) male, labelled: "Luglio, Gunong Singalang, Beccari, 1878" (MNHN). PARALECTOTYPES one specimen, sex not recorded, labelled: "Si Rambé, Modigliana, Sep. 1892" (MNHN); one male, same label as lectotype (GEN); three specimens (GEN), labelled: "Syntype. Si Rambé, Modigliana, XII-90-III-91" are not *R. gestroi* but *R. indigens*. Both localities are in Sumatra.

Description.— Length 6.2-7.0 mm. Antennal stylet acuminate; antennal Segment XI longer than broad, scarcely compressed; few basal setae on Segment X, absent from more proximal segments; antennae longer, more slender, than in related species, outer segments oblate spheroids; Segments I-X each with subapical pollinose ring; head slightly longer than wide; antennal lobe largely pollinose, with a few irregular glabrous areas; median lobe short, rather narrow, shield-shaped, its tip obtuse, opposite anterior 0.33 of eye; frontal grooves rather broad, deep, pollinose; medial margins of temporal lobe oblique, closest together posteriorly, where medial angles are narrowly separated, nearly closing frontal space posteriorly; temporal lobe 2.5 longer than wide; temporal lobe evenly rounded posteriorly, with conspicuous pollinose border; orbital groove complete, narrow; eye narrowly crescentic, 0.5 as long as temporal lobe; one temporal seta, in orbital groove posterior to eye; postorbit pilose.

Pronotum moderately elongate; length/greatest width 1.44; ovate, basal margin strongly curved; apex strongly narrowed; base moderately narrowed; lateral margins curved; median groove narrowly dilated, about 0.5 times as wide as anterior median pit; posterior median pit separated from base by 0.2 of length of pronotum; median groove basad to posterior median pit deep, margins pollinose; inner carina highest next to median groove, sloped gradually laterally to paramedian groove; medial margin of outer carina with narrow strip of pollinosity; outer carina convex, relatively broad, marginal groove linear, entire, pollinose, pronotal setae absent.

Elytra relatively short, broad, margins parallel near middle; base strongly, obliquely narrowed to humeri; apex broadly rounded, cauda not distinct; stria pollinose; sutural, parasutural scarp-like, with lateral margin much higher than medial margin; intratubercular, marginal striae impressed; base of parasutural stria bent medially; Interval III subcarinate, base forming prominent medial angle; apex forming slightly elevated preapical tubercle; apical tubercles inflated, contiguous, no pore beneath them in midline; intratubercular stria with one seta just anterior to preapical tubercle; apex of marginal stria with four setae.

Metasternum without median sulcus; transverse sulci of abdominal sterna broadly interrupted at midline, shallow, barely impressed, each sulcus with pit at medial end; female with deep lateral pit in Sternum IV; submarginal sulcus of

Sternum VI well separated from transverse sulci; tibiae moderately slender, middle, hind tibiae with two spurs, these equal in female, posterior spur smaller in male; anterior femur of male with minute ventral tooth near apex; male with all trochanters pointed; calcars narrowly triangular, acute.

This species is easily recognized by the form of the temporal lobes, which nearly meet posteriorly.

Range.— Known only from the west coast of Sumatra. In addition to the type material, we have seen three specimens with the following label: "Gunung Singgalang, Sumatra's Westkust, 1800 m. VII-1925, leg. E. Jacobson". Of these specimens, there is one male (NMNH) and one male, one female (AMS).

Rhyzodiastes (Temoana) propinquus new species
(Fig. 39)

Type Material.— HOLOTYPE female, labelled: "Nicobars, *Rhyzodiastes propinquus* Grouv." (MNHN). The latter is an unpublished species name which we are happy to adopt.

Description.— Length 6.8 mm. Antennal stylet minute, conical; antennal Segment XI as broad as long, somewhat compressed; few basal setae on Segment X, absent from more proximal segments; antennae very short, thick; outer segments short, disc-like cylinders; tufts of minor setae present on Segments IV-X; Segments I-X each with subapical pollinose ring; head slightly longer than wide; antennal lobe glabrous; median lobe short, hastate, its tip acute, opposite anterior 0.33 of eye; frontal grooves deep, glabrous; medial margins of temporal lobes curved, closest together opposite posterior part of eyes; temporal lobes appear to diverge posteriorly, because of broad posteromedial glabrous area on each temporal lobe; temporal lobe about 2.5 longer than wide; posterior margin of temporal lobe pilose; orbital groove complete; eye narrowly crescentic, approximately 0.5 as long as temporal lobe; possibly small temporal seta, in posterior part of orbital groove; postorbit pilose.

Pronotum elongate; length/greatest width 1.50; widest posterior to middle, ovate; basal margin curved, apex strongly narrowed; base moderately narrowed; lateral margins curved; median groove narrowly dilated, about 0.5 as wide as anterior median pit; posteromedian pit separated from base by 0.2 of length of pronotum; median groove based to posteromedian pit shallow, margins glabrous; inner carina highest next to median groove, sloped gradually laterally to paramedian groove; medial margin of outer carina with narrow strip of pollinosity; outer carina in dorsal view appearing narrow, because lateral 0.67 of outer carina is concave; marginal groove linear, entire, pollinose; pronotal setae absent.

Elytra moderately elongate; margins parallel near middle; base slightly narrowed to humeri; apex evenly rounded, not forming cauda; striae pollinose; sutural, parasutural striae scarp-like, with lateral margin higher than medial margin; intratubercular, marginal striae impressed, base of parasutural bent medially; base of Interval III forming prominent, pilose angle; Interval III laterad to basal angle glabrous; apex of Interval III forming rounded, elevated preapical tubercle; apical tubercles scarcely inflated, contiguous; round pore ventral to apical tubercles in midline; parasutural stria with six setae forming complete row; one seta at base of Interval III; intratubercular stria with one seta at base, one seta opposite anterior end of preapical tubercle; three or four setae in apex of marginal stria.

Metasternum with fine median sulcus; transverse sulci of abdominal sterna broadly interrupted at midline; deep, pollinose; female with deep lateral pit in Sternum IV; Sternum VI with marginal groove, posterior 0.33 impressed; tibiae moderately slender; middle, hind tibiae each with two equal spurs; male unknown.

This species is most similar to *R. bonsae* from which it can be distinguished by the apparent divergence of the temporal lobes posteriorly, the glabrous base of Interval IV, and the contiguous, scarcely inflated apical tubercles.

Rhyzodiastes (Temoana) bonsae new species
(Fig. 46)

Type Material.— HOLOTYPE female, labelled: "Sumatra, Mt. Tenggaemoes, Lampongs". (MNHN) The locality is now spelled "Gunung Tanggamus", and is near the southern tip of Sumatra.

Description.— Length 7.8 mm. Antennal stylet minute, conical; antennal Segment XI as broad as long, somewhat compressed; few basal setae on Segment X, basal setae absent from more proximal segments; antennae very short, thick; outer segments short, disc-like cylinders; Segments I-X each with subapical pollinose ring; head slightly longer than wide; antennal lobe glabrous; median lobe short, hastate, its tip acute, opposite anterior 0.33 of eye; frontal grooves deep, glabrous; medial margins of temporal lobes closest together opposite eyes, nearly parallel, very slight divergent posteriorly; medial and posterior margins of temporal lobe pilose fringe of even width; glabrous area of each temporal lobe about 2.5 longer than wide; orbital groove complete; one small, inconspicuous temporal seta in posterior part of orbital groove; postorbit with conspicuous, rather long golden pilosity.

Pronotum elongate; length/greatest width 1.54; ovate, widest near middle; lateral margins more strongly curved than in *R. propinquus*, base curved; base rather strongly narrowed; apex very strongly narrowed; median groove narrowly dilated, about 0.5 as wide as anteriomedian pit; posterior median pit separated from base by 0.2 of length of pronotum; median groove basad to posterior median pit shallow, margins glabrous; inner carina highest next to median groove, sloped gradually laterally to paramedian groove; medial margin of outer carina with narrow strip of pollinosity; outer carina in dorsal view appearing narrow, because lateral 0.67 of outer carina is concave; marginal groove linear, pollinose, entire; pronotal setae absent.

Elytra moderately elongate; margins parallel near middle; base slightly narrowed to humeri; apical tubercles protruding, forming broad but distinct cauda; sutural stria with very narrow, inconspicuous line of pollinosity; remaining striae with broader, more conspicuous pollinose lines; sutural, parasutural striae scarp-like, with lateral margin higher than medial margin; intratubercular, marginal striae very shallow, scarcely impressed; base of parasutural stria bent medially; base of Interval III forming prominent pilose medial angle; latter connected to humerus by band of pollinosity crossing base of Interval III; apex of Interval III forming low preapical tubercles, these more rounded, further apart than *R. propinquus*; apical tubercles prominent, inflated, separately rounded medially, nearly touching at one point, medial surfaces pollinose; large rounded pore ventrad to them in midline; parasutural stria with row of about 10 setae, base of this row follows medially bent portion of parasutural stria to base of sutural stria, while most posterior setae of this row is displaced slightly laterad to stria, arising from medial surface of preapical tubercle; one seta at base of Interval III laterad to parasutural stria; one or two setae on preapical tubercle; one or two setae in apex of intratubercular stria; several setae near apex of marginal stria.

Metasternum with faint trace of median sulcus in posterior 0.5; abdominal sterna with transverse sulci well defined but glabrous, broadly interrupted in midline; small pit at medial end of each sulcus; female with deep, round lateral pit on Sternum IV; Sternum VI with transverse sulci, narrow marginal groove, disc not impressed; tibiae moderately slender; middle hind tibiae each with two equal spurs; male unknown.

Among species with the median groove narrowly dilated, this species may be recognized by the nearly parallel medial margins of the temporal lobes and by the inflated, separately rounded apical tubercles.

It is a pleasure to name this species for Madame Andree Bons, of the National Museum of Natural History in Paris, in gratitude for the aid that she has given to us and to many other coleopterists over the years.

THE FAIRMAIREI GROUP

There are four species in this group, all from the mainland of Southeast Asia. Among the species with a tuft of minor setae on Segment IV, they are easily recognized by the greatly dilated median groove of the pronotum.

Phylogeny.— The relationships within the group are relatively obvious. *R. fairmairei* differs from all the rest in the great enlargement of the posteriomedian pit of the pronotum, and in the absence of temporal and elytral setae. It is probably only distantly related to the three remaining species, which have the median groove of even width, not dilated by the enlargement of the posteriomedian pit; and which have one or more temporal setae, and, in most specimens, elytral setae. Among these three species, the two Vietnamese species appear to be very closely related, with *R. spissicornis* of Malaya being more distant. The latter species has a median sulcus on the metasternum, equal tibial spurs, setae in the sutural stria, in the fourth interval, and on the apical tubercle, and the head elongate, with margins oblique posterior to the eyes. In the two Vietnamese species, the median sulcus is absent, the tibial spurs are unequal, and the elytral setae are limited to the parasutural stria and the apex of the marginal stria, or else are absent.

Rhyzodiastes (Temoana) fairmairei Grouvelle 1895b NEW COMBINATION (Fig. 47)

Rhyzodiastes fairmairei Grouvelle 1895b: 762-763.

Clinidium fairmairei (Grouvelle) Grouvelle 1903.

Rhyzodiastes fairmairei (Grouvelle 1895b) Bell and Bell 1978.

(Incorrect citation: Grouvelle originally described the species in *Rhyzodiastes*.)

Type Material.— HOLOTYPE female, labelled: "Carin Cheba, 900-1100 m., L. Fea, V-XII-88" (MNHN). In the original description, the locality is given as "Montagnes des Carin, district des Carin Cheba". It is in eastern Burma.

Description.— Length 7.0 mm. (our measurement; Grouvelle gives the length as 6.5 mm). Antennal stylet acute, rather long; antennal Segment XI somewhat compressed, as wide as long; outer antennal segments very short, thick, cylindrical, disc-like; basal setae absent; Segments I-X each with subapical pollinose ring; latter interrupted ventrally on Segments IV-X by tuft of minor setae; head 1.25 longer than wide; antennal lobe glabrous; median lobe short, hastate, tip acute, extending slightly posterior level of anterior margin of eye; frontal grooves rather broad, deep, pollinose; antennal groove oblique, deep, pollinose; temporal lobe three times longer than wide; medial margins curved, closest together opposite posterior margin of eye; posterior margin rounded, broadly fringed with pilosity, latter extended obliquely anteriorly along medial margin; orbital groove complete, pollinose; eye crescentic, rather short, about 0.33 as long as temporal lobe; temporal seta absent.

Pronotum elongate, length/greatest width 1.51; oval, widest at middle, lateral margins curved; base, apex both narrowed; base strongly curved; median groove very broad, resembling keyhole, posterior portion (posteriomedian pit) round, about 0.33 of width of pronotum; anterior portion with parallel margins, about 0.2 of width of pronotum; inner carinae broad, sloped laterally; medial margin of outer carina with narrow strip of pollinosity; in dorsal view, outer carina appears narrow, curved; outer carina with lateral surface concave, bounded ventrally by poorly defined marginal groove; submarginal groove, pronotal setae absent.

Elytra elongate, rather narrow; lateral margins parallel near middle; humeri abruptly, obliquely narrowed; sutural, parasutural stria finely punctate, impressed, scarp-like, with lateral margin of each much higher than medial margin, base of parasutural stria bent medially; intercalary, marginal striae rather coarsely punctate, scarcely impressed except at apex; subapical tubercle slightly elevated; apical tubercles inflated, contiguous at midline; elytral setae entirely absent.

Metasternum without median sulcus; transverse sulci of abdomen broadly interrupted at midline; sulci largely glabrous, each with median, lateral pit; lateral pit of Sternum IV enlarged in female; submarginal sulcus of Sternum VI widely separated from transverse sulcus at base, latter scarcely impressed, appearing as pair of pits on either side; middle and hind tibia each with spur equal. Male unknown.

The broad, median groove of this species resembles a keyhole, and is unique within the genus.

Rhyzodiastes (Temoana) spissicornis Fairmaire 1895 NEW COMBINATION (Fig. 48)

Rhyzodiastes spissicornis Fairmaire 1895: 11-12.

Clinidium spissicorne (Fairmaire) Grouvelle 1903.

Rhyzodiastes spissicornis (Fairmaire) Bell and Bell 1978.

(Incorrect citation; Fairmaire originally described the species in *Rhyzodiastes*.)

Type Material.— LECTOTYPE male, labelled: "Puolo Pinang, Raffray, Ty., voisin de parumcostatum de Fairm de Madagascar" (MNHN). PARALECTOTYPE female, labelled: "Singapore" (MNHN).

Description.— Length 5.5-7.0 mm. Antennal stylet small, conical; antennal Segment XI compressed, as broad as long; basal setae absent; antennae very short, thick; outer segments very short cylinders, 2.5 wider than long; tufts of minor setae present on Segments IV-X; Segments I-X each with subapical pollinose ring; head elongate, length/width 1.5; antennal lobe glabrous; medial lobe very short, shield-shaped, its tip obtusely pointed, at level with anterior margin of eye; frontal grooves deep, glabrous; medial margins of temporal lobe curved, closest together opposite middle of eye; temporal lobes divergent posteriorly; temporal lobe three times longer than wide; posterior half of medial margin, posterior margin of temporal lobe fringed with pilosity; orbital groove complete, sinuate; eye crescentic, short, 0.5 as long as temporal lobe; one small temporal seta, halfway between posterior end of eye, occipital angle; postorbital pilose.

Pronotum elongate; length/greatest width 1.55; widest posterior to middle, ovate; basal margin curved; base moderately narrowed; apex strongly so; lateral margins curved; median groove dilated, about 10 times longer than broad, gradually narrowed anteriorly; anterior median pit separated from apex of pronotum by about 0.1 of pronotal length; posterior median pit separated from base by about 0.33 of length of pronotum; median groove very shallowly impressed in front of anterior median pit and behind posterior median pit; inner carina highest next to median groove, sloped gradually laterally to paramedian groove; medial margin of outer carina with narrow strip of pollinosity; outer carina in dorsal view appearing narrow, because lateral 0.67 of outer carina is concave; marginal groove represented only by inconspicuous line of minute pollinosity at ventral margin of concavity; pronotal setae absent.

Elytra elongate; margins parallel near middle; narrowed near humeri; latter prominent, tooth-like in dorsal aspect; apex evenly rounded, not forming cauda; all striae scarp-like, with lateral margin higher than medial one; sutural, parasutural, marginal impressed, pollinose; intratubercular with base, apex impressed, pollinose, middle not pollinose, scarcely impressed; base of parasutural stria bent medially; base of Interval III forming prominent medial angle, latter

fringed with pilosity; base of Interval III with prominent lateral swelling just posterior to humeral angle; apex of Interval III forming narrow, elevated preapical tubercle; apical tubercles slightly inflated, contiguous; sutural, parasutural stria and Interval IV each with complete row of many setae; posthumeral elevation, apical tubercle with setae; apex of marginal stria with several setae.

Metasternum with median sulcus; transverse sulci of abdomen broad, deeply impressed, each with narrow transverse line of pollinosity; transverse grooves well separated at midline; those of Sternum VI slightly oblique, well separated from submarginal groove; lateral pit of Sternum IV enlarged in female; tibiae thick; middle, hind tibiae each with two equal spurs; ventral surface of anterior femur of male with many minute tubercles, but without ventral tooth; male with front, hind trochanters pointed; calcars acute, triangular.

This species can be recognized by the dilated median groove in combination with the great development of elytral setae. The elongate head, with relatively short eyes, also separates it from the two species from Viet Nam.

Range.— Malay Peninsula. In addition to the type material we have seen the following specimens: one female, labelled: "Perka" (BMNH); one female, labelled: "Penang" (BMNH); one female, labelled: "Malaya, Kuala Lumpur, 90 m. VI-7-1962, coll. E. S. Ross and D. Q. Cavagnaro" (CAS), one male, labelled: "P. Penang, Raffray" (GEN), one male, labelled: "P. Penang, 600-800 M., Loria e Fea" (GEN), also one male without locality label (MNHN).

Rhyzodiastes (Temoana) alveus new species

(Figs. 49, 52)

Type Material.— HOLOTYPE male, labelled: "Hoa Binh, Tonkin, de Cooman, B.M. 1929-299" (BMNH). PARATYPES two males, same label as holotype (BMNH); one male, three females, same label as holotype except that acquisition number reads "B,M, 1925-251" (BMNH).

Description.— Length 5.0-6.8 mm. Antennal stylet small, conical; antennal Segment XI not compressed, longer than wide, basal setae absent; antennae moderately short, thick; outer segments oblate spheroids, less than two times wider than long; tufts of minor setae present on Segments IV-X; pollinosity in some specimens present on all antennal segments, in other specimens limited to Segments I-III; head slightly longer than wide; median lobe short, shield-shaped, its tip acute, opposite anterior margin of eye; frontal grooves deep, glabrous; medial margins of temporal lobes curved, closest together opposite middle of eye; posterior 0.5 of medial margin, lateral margin posterior to eye, with long pilosity; glabrous area of temporal lobe three times longer than wide, tapered to point posteriorly, its medial margin concave opposite posterior 0.5 of medial margin; orbital groove complete, margin with lateral pilosity posterior to eye; eye narrow, crescentic, larger than *R. spissicornis*, 0.67 as long as temporal lobe; one small temporal seta opposite posterior margin of eye; postorbit pilose.

Pronotum moderately elongate; length/greatest width 1.44; widest at middle; base, apex equally narrowed; lateral margins moderately curved; base moderately curved; median groove dilated, its deep portion five times longer than wide, margins nearly parallel; posterior median pit separated from base by about 0.25 of length of pronotum; median groove shallowly impressed in front of anterior median pit, behind posterior median pit; inner carina highest next to median groove, sloped gradually to paramedian groove; medial margin of outer carina with narrow strip of pollinosity; fine line of pollinosity in concavity of outer carina, distant from lateral margin and notopleural suture (Fig. 52); outer carina, in dorsal view, appearing narrow because lateral 0.67 of outer carina is concave; pronotal setae absent.

Elytra moderately elongate; margins parallel near middle, narrowed slightly near humeri; apex evenly rounded, not forming cauda; all striae scarp-like, with lateral margin much higher than medial one; all striae impressed, with very fine line of minute pollinosity; marginal stria interrupted posteriorly, apical portion detached, on ventral surface of apical tubercle; base of parasutural stria bent medially; base of Interval III forming prominent pilose medial angle; base of Interval III without lateral swelling; apex of Interval III forming narrow, elevated preapical tubercle; in posterior view, posterior margin of preapical tubercle emarginate, apex overhanging base; apical tubercles slightly inflated, contiguous; apex of marginal stria with several setae; elytron otherwise without setae.

Metasternum without median sulcus; transverse sulci of abdominal sterna narrow, not interrupted at midline, with pair of dilated pits on either side of midline; those of Sternum VI connected laterally to base of marginal groove; both sexes with lateral pit in Sternum IV, that of female larger than that of male; tibiae relatively slender; spurs of middle and hind tibiae unequal, medial one about 0.5 as long as lateral one; male with ventral tooth on anterior femur; male with hind trochanter pointed; calcars blunt, middle one narrow, hind one triangular, its proximal margins slightly angulate.

The short head, lack of a median metasternal sulcus, and greatly reduced elytral setae separate this species from *R. spissicornis*. The absence of setae from the parasutural stria and the broader median groove separate it from *R. fossatus*.

Range.— Northern Viet Nam, west and north of Hanoi. In addition to the type series, we have seen the following specimens: two females, labelled: "N. Viet Nam, northwest of Tam Dao, Shou-Zuong, 1-2-1962, 200, 300 m., Kabakov" (LEN); one female, same data, 300 m., 20-2-1962 (LEN); one female, same data, 31-1-1962 (LEN); one male, labelled: "North Viet Nam, hills 50 km. NW of Thai-Nguyen, 19-12-1962, 400 m. Kabakov" (LEN); one male, same data, except 9-3-1963, 300 m. Kabakov (LEN); one female, same data, except 8-11-1963, Kabakov (LEN).

Variation.— The type series, from southwest of the Son Koi (Red River), have subapical pollinose rings on all antennal segments, and have a pollinose area on the lateral surface of the hind, and in most specimens, of the middle tibia. Specimens from northeast of the Song Koi (Thai-Nguyen, Tam Dao) have pollinose rings only on antennal segments I and II, and lack pollinosity on the lateral surfaces of the middle and hind tibiae, although there is a pollinose line on the posterior face of the tibia. The latter is also present in the specimens from Hoa Binh. Further collecting may demonstrate that the northeastern populations represent a separate species or subspecies.

Rhyzodiastes (Temoana) fossatus new species
(Figs. 50, 53, 54)

Type Material.— HOLOTYPE male, labelled: "N. VIET NAM, hills s.w. Kui Chau, 300 m. 14-1-1963, Kabakov" (LEN). PARATYPES five males, five females, same locality, several dates from 12-1-1963 to 15-11-1963 (LEN). The locality is in the north part of the former Annam, about 200 Km. south of Hanoi.

Description.— Length 5.6-7.0 mm. Antennal stylet small, conical; antennal Segment XI slightly compressed, as wide as long; basal setae absent; antennae moderately thick, short; outer segments oblate spheroids, less than two times wider than long; tufts of minor setae present on Segments IV-X; Segments I-X with subapical pollinose rings, in some specimens interrupted near some of the apical setae; head slightly longer than wide; median lobe short, shield-shaped, tip acute, opposite anterior margin of eye; frontal grooves deep, glabrous; medial margins of temporal lobes curved closest together opposite middle of eye; posterior 0.5 of medial margin, lateral margin posterior to eye, with long pilosity; glabrous area of temporal lobe three times longer than wide, tapered to point posteriorly, its medial margin oblique, straight or nearly so opposite posterior 0.5 of medial margin; orbital groove complete, merging with lateral pilosity posteriorly; eye narrow, crescentic, 0.67 as long as temporal lobe; one small temporal seta opposite posterior margin of eye; postorbit pilose.

Pronotum moderately elongate; length/greatest width 1.42; widest at middle; base, apex equally narrowed; lateral margins moderately curved; base moderately curved, median groove dilated, but narrower than in *R. alveus*, deep portion six times longer than wide, margins nearly parallel; floor of groove minutely pollinose with narrow glabrous median line; posterior median pit separated from base by about 0.20 of length of pronotum; median groove shallowly impressed in front of anterior pit, behind posterior median pit; inner carina highest next to median groove, sloped gradually to paramedian groove; medial margin of outer carina with narrow strip of pollinosity; line of pollinosity along lateral margin of pronotum just dorsal to notopleural suture (Fig. 53); outer carina, in dorsal view, appearing narrow because lateral 0.67 of outer carina is concave; pronotal setae absent.

Elytra moderately elongate; margins parallel near middle, narrowed slightly near humeri; apex evenly rounded, not forming cauda; all striae scarplike, with lateral margin much higher than medial margin; all striae impressed, with line of pollinosity; marginal stria interrupted posteriorly, apical portion detached, on ventral surface of apical tubercle; base of parasutural stria bent medially; base of Interval III forming prominent pilose medial angle; base of Interval III without lateral swelling; apex of Interval III forming narrow, elevated preapical tubercle; in posterior view, posterior margin of preapical tubercle emarginate, apex overhanging base; apical tubercles slightly inflated, contiguous; parasutural stria with five to eight setae, in a few specimens forming complete row, in most specimens with a gap near middle; apex of marginal stria with several setae (Fig. 54).

Metasternum without median sulcus; transverse sulci of abdominal sterna narrow, not interrupted at midline, with pair of dilated pits on either side of midline; those of Sternum VI connected laterally to base of marginal groove of Sternum VI; both sexes with lateral pit in Sternum IV, that of female larger than that of male; tibiae relatively slender; spurs of middle, hind tibiae unequal, medial one about 0.5 as long as lateral one; male with ventral tooth on anterior femur; male with hind trochanter pointed; calcaria as in *R. alveus*; lateral surface of tibia in both sexes with extensive pollinose area containing glabrous tubercles.

This species is close to *R. alveus*, from which it differs most conspicuously in the presence of setae in the parasutural stria and in having a narrower, minutely pollinose median groove on the pronotum.

SUBGENUS *RHYZOSTRIX* NEW SUBGENUS

Type species.— *Rhyzodes maderiensis* Chevrolat 1873a.

Description.— Antennal stylet present, though minute in some species; tufts of minor setae present on Segments IV-X; clypeal setae present; compound eye relatively broad, oval; posterior margin of temporal lobe broadly pilose; gena with curved band of pollinosity ventrad to eye; temporal seta absent; inner carina of pronotum sloped gradually to paramedian groove; pollinosity limited to narrow line on medial slope of outer carina; base of pronotum with pollinose border; paramedian grooves straight to slightly curved; outer carina not greatly enlarged or broadened at middle; pronotal setae absent; intercalary stria absent; elytral striae coarsely punctate.

The large, oval eyes are diagnostic of this subgenus. Otherwise, it is superficially similar to *Temoana*. The very coarsely punctate elytral striae will separate it from all except *R. (T.) sulcicollis*. The appearance is quite different from *Rhyzodiastes sensu stricto*, the other subgenus found in South America. The latter genus has narrow, costate outer carinae, smaller, more crescentic eyes, and broadly pollinose paramedian and marginal grooves. However, the two South American subgenera have some characters in common, such as pollinosity of the gena in a curved, c-shaped band, elytral striae coarsely punctate, and posterior margin of temporal lobe with very broad band of pollinosity. Perhaps they are related to one another.

Clinidium quadristriatum (Chevrolat) was used by Vulcano and Pereira (1975b) as the name for a species of this genus. Their species is probably distinct from any known to us, but, as indicated below, there is doubt as to whether *C. quadristriatum* is the correct name for it. They illustrate another species under the name *C. integrum* Grouvelle, but this is not the species described by Grouvelle (a *Clinidium s. str.*), but is probably yet another undescribed *Rhyzostrix*.

Rhyzostrix is found in South America, in the Amazon Basin and Guiana and south along the coast to Rio de Janeiro. It is largely allopatric to *Rhyzodiastes sensu stricto*.

Phylogeny.— Of the species known to us, *R. menieri* and *R. maderiensis* appear to be closely related. If the convex, setose sutural interval is regarded as a synapomorphy, *R. nitidus* is closer to the two preceding than to *R. davidsoni*. If the flat non-setose sutural interval of the latter species is an apomorphy, *R. davidsoni* may be merely the most specialized species, and not the most phylogenetically distinct one. Current data are insufficient to choose between these possible phylogenies or to place *R. quadristriatus* in the phylogeny.

KEY TO SPECIES

- 1 Elytral Intervals I-III undulating, irregular, invaded by enlarged strial punctures *R. quadristriatus* (Chev), p. 49
- 1' Elytral Intervals I-III not undulating, irregular 2
- 2 (1') Sutural interval flat, without setae; antenna without basal setae; hind calcar cultrate *R. davidsoni* new species, p. 49
- 2' Sutural interval convex, with two to four setae near apex; basal setae of antenna present; hind calcar straight 3
- 3 (2') Punctures of sutural, parasutural striae very coarse, nearly as broad as Interval II; Stria III with pilosity limited to punctures; tip of preapical tubercle slightly dentate, its posterior margin emarginate; Sternum VI of female not impressed *R. nitidus* new species, p. 52
- 3' Punctures of sutural, parasutural striae smaller, less than 0.5 of width of Interval II; Stria III with continual pollinosity; tip of preapical tubercle not dentate, rounded posteriorly; Sternum VI of female impressed, with

- tubercle at midline 4
- 4 (3') Sternum VI of female with pollinose pit posterior to small tubercle;
Sternum IV without lateral pits in the female *R. menieri* new species, p. 52
- 4' Sternum VI of female with pair of pollinose areas or crescent area posterior
to tubercle; Sternum IV of female with lateral pits evident, though small
..... *R. maderiensis* (Chevrolat), p. 53

Rhyzodiastes (Rhyzotrix) quadristriatus (Chevrolat 1873a) NEW COMBINATION

Rhyzodes quadristriatus Chevrolat 1873a: 211.

Clinidium quadristriatum (Chevrolat) Grouvelle 1903.

Rhyzodiastes quadristriatus (Chevrolat) Bell and Bell 1978.

Type Material.— HOLOTYPE (sex not stated) according to the original description "Cayenna ex museo Banoni". We have not been able to locate the type, which was not studied by Vulcano and Pereira (1975b). "Cayenne" refers to French Guiana.

Description.— Vulcano and Pereira (1975b) assigned a specimen from Brazil (Pará, Taperinha perto de Santarém, 1-10, VII. 1927 Zerny leg.) to this species. We have not studied this specimen. As indicated in our key, it differs from all species seen by us in having Intervals I-III undulating and irregular, invaded by enlarged punctures of sutural and parasutural striae. However, there is doubt as to whether the Chevrolat name really applies to this specimen. The original description does not mention the undulating, irregular intervals. Grouvelle (1903) did cite undulating, irregular intervals as characteristic of this species, and of *R. maderiensis* as well, but did not state that he had studied the type of *R. quadristriatus*. Unless the type can be located, *R. quadristriatus* should probably be regarded as a *nomen dubium*, and the specimen attributed to it by Vulcano and Pereira should be given a new name.

Rhyzodiastes (Rhyzotrix) davidsoni new species
(Figs. 51, 55, 62, 64)

Type Material.— HOLOTYPE male, labelled: "Brazil, Amazonas, 1 km. W. Taruma Falls, 100 m., 11-I-1981, coll. R. Davidson" (CMP). PARATYPES three males, three females, same data as holotype (CMP); one male, labelled: "Manaus, Amazonas, Brasil, VIII-1962, coll. K. Lenko" (MZSP).

Description.— Length 5.9-6.8 mm. Antennal stylet minute; basal setae of antenna absent; head longer than wide; frontal grooves very narrow, shallow; median lobe longer than in related species, its tip even with middle of eye; gena with horizontal pollinose line just below eye, but without curved ventral continuation.

Pronotum short for subgenus, length/greatest width 1.53; suboval, with apex more truncate, hind angles more distinct than in other members of subgenus; widest just posterior to middle; lateral margins constricted just anterior to middle, width anterior to constriction almost equal to greatest width; marginal groove strongly abbreviated posteriorly, ending just posterior to middle of pronotum.

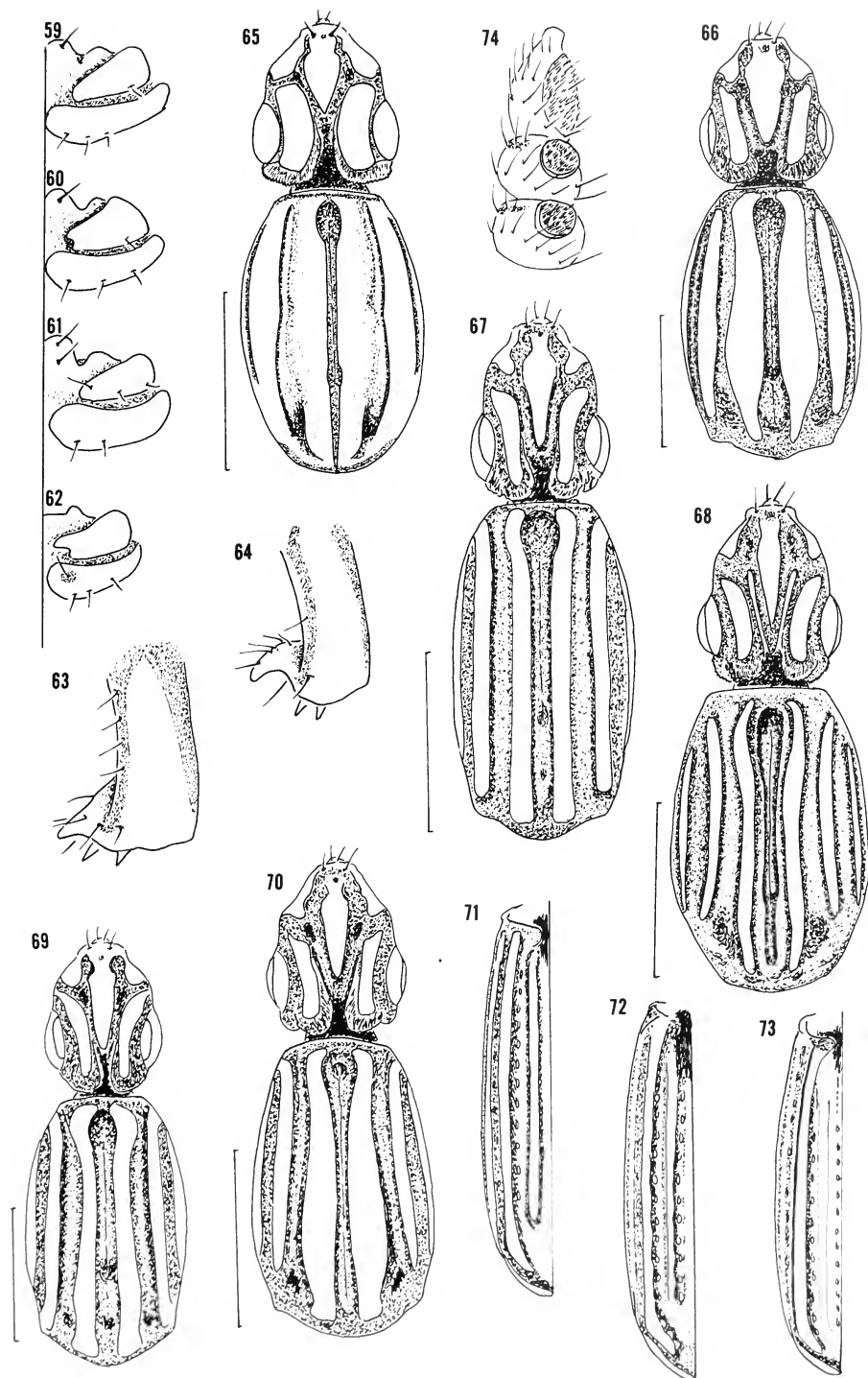
Elytra elongate, lateral margins parallel through most of length; humeri narrowed; sutural stria, fine with about 10 moderately fine punctures; parasutural striae impressed, wider than others, with about 10 coarse punctures; intercalary, marginal striae impressed, rather finely punctate; sutural interval completely flat (Fig. 62); second interval convex, subcarinate; third interval elevated above parasutural stria, medial margin broadly pollinose; third intervals strongly convergent anteriorly; apex of third interval forming elevated preapical tubercle, latter with posterior margin strongly emarginate; preapical tubercles dentate, nearly contiguous in midline; apical tubercle with one or two setae; apex of marginal stria with several setae; sutural interval without setae.

Metasternum with complete, deep, median sulcus; abdominal sterna each with narrow, coarsely punctate transverse sulcus; Sulci III-IV complete, V, VI complete or narrowly interrupted in midline; submarginal sulcus of Sternum VI of female with expanded pit at either side (Fig. 55), male without such expanded pit; middle, hind femora of male angulate beneath; hind trochanter pointed in male; middle calcar very narrow, straight, acute; hind calcar elevated above tibial spurs, strongly cultrate (Fig. 64).

The flat sutural interval, entirely without setae, differentiates this species from the rest of the subgenus. The strongly dentate preapical tubercles, short pronotum with distinct hind angles and truncate apex, and the curved, hooklike hind calcars, are also diagnostic.

Range.— In addition to the type series we have seen three males, three females, labelled: "Brasil, Amazonas, BR. 174, Km. 18, 5-XII-1979, Elias Brasil" (INPA).

Plate 6. Figs. 59–65. Genus *Rhyzodiastes*, new Subgenus *Rhyzostrix*. Figs. 59–62, Right elytron, posterior aspect; Fig. 59, *R. (R.) menieri* new species; Fig. 60, *R. (R.) nitidus* new species; Fig. 61, *R. (R.) maderiensis* (Chevrolat); Fig. 62, *R. (R.) davidsoni* new species; Figs. 63–64, Hind tibia, apex, male; Fig. 63, *R. (R.) maderiensis* (Chevrolat); Fig. 64, *R. (R.) davidsoni* new species; Figs. 65–70, Head and pronotum, dorsal aspect; Fig. 65, *R. (R.) maderiensis* (Chevrolat). Figs. 66–74. Subgenus *Rhyzodiastes sensu stricto*. Fig. 66, *R. (s. str.) pentacyclus* new species; Fig. 67, *R. (s. str.) liratus* (Newman); Fig. 68, *R. (s. str.) parumcostatus* (Fairmaire); Fig. 69, *R. (s. str.) suturalis* new species; Fig. 70, *R. (s. str.) costatus* (Chevrolat); Figs. 71–73, Left elytron, dorsal aspect; Fig. 71, *R. (s. str.) liratus* (Newman); Fig. 72, *R. (s. str.) suturalis* new species; Fig. 73, *R. (s. str.) costatus* (Chevrolat); Fig. 74, Antennal Segments IX–XI, *R. (s. str.) pentacyclus* new species.



Variation.— One of the females from Taruma Falls has a tubercle in the middle of Sternum VI of the abdomen, while the other two females lack any trace of a tubercle. This might prove to be a specific character; however, the tuberculate and one of the nontuberculate females were taken *in copula* with apparently identical males. It is possible that the females are morphs of a polymorphic population, analogous to *Clinidium veneficum* Lewis.

In addition to type material, we provisionally assign to this species a male, labelled: "Taracua, Rio Uaupés, Amazonas, Brasil, VIII-1964 Pereira and Machado" (MZSP). It conforms to the description of *R. davidsoni* in most respects, but has a low second interval, only slightly more convex than the sutural interval. The hind trochanter is less distinctly pointed than in the type series. This locality is far to the west of Manaus, and is near the Colombian border. This form might be a distinct, though closely related species, a subspecies, or the differences might be clinal. A decision must await collections in the intervening area.

Rhyzodiastes (Rhyzotrix) nitidus new species
(Figs. 56, 60)

Type Material.— HOLOTYPE male, labelled: "Santarem, Brazil, Acct. No. 2966" (CMP). PARATYPES one male, one female, same data as holotype (CMP); two males, one female, labelled: "Rio de Jan., Brazil, Acct. No. 2966" (CMP); one male, one female, labelled: "Amaz., Pará" (MNHN). The female of this pair is labelled: "*Clinidium nitidum* Grouv.", an unpublished name.

Description.— Length 6.0-7.2 mm. Antennal stylet small, narrowly conical; basal setae present on Segment VII-X; head longer than wide; frontal grooves moderately wide, shallow; median lobe very short, its tip opposite anterior margin of eye; gena with curved pollinose line.

Pronotum oval, elongate; length/greatest width 1.59; widest near middle; base strongly curved; apex moderately curved; hind angles indistinct; marginal groove over 0.6 as long as pronotal margin, separated from base, apex by 0.2 of length of margin.

Elytra elongate, lateral margins parallel through most of length; humeri narrowed; sutural stria impressed, coarsely punctured, punctures nearly as wide as Interval II; parasutural stria deeply impressed, coarsely punctured, both striae with about 8 elongate punctures; intratubercular, marginal striae broad, impressed, with medial margins sloped gradually from intervals, coarsely punctate, though less coarse than punctures of sutural, parasutural striae; sutural intervals together convex (Fig. 60); Interval II convex, lower than I or III; Interval III elevated above parasutural stria, medial margin broadly pollinose; bases of third intervals weakly convergent; apex of third interval thickened, forming elevated preapical tubercle, latter with posterior margin emarginate; preapical tubercles weakly dentate, separated from one another by width of one sutural interval; sutural interval with two to four setae in apical 0.5; apical tubercle with one seta; apex of marginal stria with several setae.

Metasternum with complete median sulcus; abdominal Sterna III-VI each with narrow, coarsely punctate transverse sulcus, narrowly interrupted at midline; female with deep, large, round lateral pit on Sternum IV (Fig. 56); male without lateral pit; Sternum IV alike in both sexes, not impressed; middle, hind calcars similar, narrow, straight, acute.

The very coarse punctures of the sutural and parasutural striae and the separated pilose punctures of Stria III are distinctive of this species. The dentate preapical tubercle will separate it from *R. menieri* and *R. maderiensis*, while the convex and setose sutural interval separates it from *R. davidsoni*.

Range.— Coastal lands of Brazil, from the lower Amazon south to Rio de Janeiro.

Rhyzodiastes (Rhyzotrix) menieri new species
(Figs. 57, 59)

Type Material.— HOLOTYPE female, labelled: "GUYANE, Haut-Carsevenne, F. Geay, 1898" (MNHN).

Description.— Length 7.1 mm. Antennal stylet minute, conical; basal setae present on Segments VII-X; head slightly longer than wide; frontal grooves shallow, moderately narrow; median lobe with tip opposite anterior 0.25 of eye; gena with curved pollinose line.

Pronotum oval, elongate, length/greatest width 1.57, widest just posterior to middle; margin, marginal groove, paramedian groove slightly constricted near middle; base strongly curved; apex moderately curved; hind angles indistinct; marginal groove of pronotum nearly complete, separated from basal pollinosity by 0.1 of length of pronotum.

Elytra elongate, lateral margins parallel through most of length; humeri narrowed; sutural stria deeply impressed, with about 10 punctures, latter less than 0.25 as wide as Interval II; parasutural stria impressed, with 10 punctures; intratubercular, marginal striae broad, impressed, with medial margins sloped gradually from intervals, rather finely punctate; sutural intervals together, convex (Fig. 59); Interval II convex, lower than I or III; Interval III elevated above parasutural stria, medial margin broadly pollinose; bases of third intervals weakly convergent; apex of third interval thickened, forming elevated preapical tubercle, latter with posterior margin rounded, not dentate; preapical tubercles separated by combined width of both sutural intervals; sutural interval with two setae near apex; apical tubercle with one seta; apex of marginal stria with several setae.

Metasternum with complete shallow median sulcus; abdominal Sterna III-VI, each with coarsely punctate transverse sulcus, narrowly interrupted at midline; female without lateral pit on Sternum IV (Fig. 57); Sternum VI in female impressed in apical 0.33; impression bounded anteriorly in midline by small tubercle; small median pollinose pit posterior to tubercle; male unknown.

This species is close to *R. maderiensis*, but the female differs in having a smaller tubercle with one median pollinose pit posterior to it on Sternum VI and in lacking the lateral pit on Sternum IV.

It is a pleasure to name this species for Dr. Jean-Jacques Menier of the Muséum National d'Histoire Naturelle in appreciation of his aid in our study of *Rhysodini*.

Rhyzodiastes (Rhystrix) maderiensis (Chevrolat 1873a) NEW COMBINATION
(Figs. 58, 61, 63, 65)

Rhyzodes maderiensis Chevrolat 1873a: 211-212.

Clinidium maderiensis (Chevrolat) Grouvelle 1903.

Rhyzodiastes maderiensis (Chevrolat) Bell and Bell 1978.

Type Material.— HOLOTYPE (sex not specified), according to the original description, labelled "Madereo", and collected by Lethierry. The type locality refers to the Rio Madeira, a major tributary of the Amazon River. We have not studied the type specimen but Vulcano and Pereira (1965b) have seen the type from the Vienna Museum collection. The figure and description agree with specimens seen by us, and on which the description below is based.

Description.— Length 6.0-7.0 mm (according to Vulcano and Pereira, five to eight mm). Antennal stylet minute, conical; basal seta present on Segments VI-X or VII-X; head longer than wide; frontal grooves shallow, moderately narrow; median lobe with tip opposite anterior 0.25 of eye; gena with curved pollinose line.

Pronotum oval, elongate; length/greatest width averaging 1.60, ranging from 1.55-1.65, widest just posterior to middle, margin slightly constricted at middle, marginal, paramedian grooves slightly sinuate opposite constriction; base strongly curved; apex moderately curved; hind angles indistinct; marginal groove of pronotum less complete than in *R. menieri*, separated from basal pollinosity by 0.2 or more of length of pronotum.

Elytra elongate, lateral margins parallel through most of length; humeri narrowed; sutural stria deeply impressed, with about 10 punctures, latter less than 0.25 as wide as Interval II; parasutural stria impressed; with about 10 punctures like those of sutural stria; intratubercular, marginal stria broadly impressed, with medial margin sloped gradually from intervals, rather finely punctate; sutural intervals together convex (Fig. 61); Interval II convex, lower than I or III; Interval III elevated above parasutural stria, medial margin broadly pollinose; bases of third intervals weakly convergent; apex of third interval thickened, forming elevated preapical tubercle, latter with posterior margin rounded, not dentate; preapical tubercles separated by combined width of both sutural intervals; sutural interval with three to five setae in apical 0.67; apical tubercle with one seta or without; apex of marginal stria with several setae.

Metasternum with median sulcus incomplete, anterior part effaced; abdominal Sterna III-VI narrow, coarsely punctate; all sulci narrowly interrupted in midline in female; sulci of Sterna III, IV not interrupted in male; Sternum VI not impressed in male; Sternum VI of female with apical 0.33 deeply impressed, impression bounded anteriorly in midline by tubercle; pair of median pollinose pits posterior to tubercle (Fig. 58); male with femora obtusely angulate ventrally; both pairs of calcaria acute, triangular, straight; hind calcar larger, more broad based than middle one (Fig. 63).

R. maderiensis is close to *R. menieri* but differs in the female having a larger tubercle on Sternum IV with paired pollinose pits or a crescent shaped pit and in having a lateral pit on Sternum IV.

Range.— We have seen the following specimens all from Manaus, Brasil: three males, four females, Manaus, 1 km. W. Taruma Falls, 100 m., 11-I-1981, coll. R. Davidson, (CMP); two males, three females, VIII, 1962, coll. K. Lenko (MZSP); one male, one female, 26-VIII-1962, coll. W. L. Brown (MZSP). Manaus is about 125

kilometers west of the mouth of the Rio Madeira. The latter is listed as the type locality, but there is no information as to where on the river it was taken.

SUBGENUS *RHYZODIASTES SENSU STRICTO*

Type species.— *Rhyzodes parumcostatus* Fairmaire 1868.

Description.— Antennal stylet compressed, broad, obliquely truncate, resembling chisel blade; tufts of minor setae begin on Segment IV, V, or VI; clypeal setae present; eye crescentic, narrow in most species, broad in one species; gena with curved band of pollinosity; pronotum elongate; inner carina with lateral margin sharply defined; paramedian groove broad, pollinose, at least 0.5 as wide as outer carina; marginal groove broad, sharply defined, pollinose, visible in dorsal view; pronotal setae absent; elytron with intercalary stria absent; elytral intervals, especially Interval III costate (least so in *R. pentacyclus*); elytral setae absent; metasternum with median sulcus.

This subgenus is easily recognized by the broad, pollinose paramedian grooves, narrow, sharply defined inner carinae, and broad, chisel-like antennal stylet. It is found in southern and eastern Brazil, in the coastal mountains and the Mato Grosso, and reaches northern Argentina. It apparently does not penetrate the Amazon Basin.

Phylogeny.— *R. pentacyclus* is the most distinctive species and probably represents the sister group to the remaining species. The elytral intervals are not costate, while among the remaining species at least Interval III is strongly costate. In this character state, *R. pentacyclus* is obviously the least modified member of the subgenus. The absence of tufts of minor setae from antennal Segments IV and V is probably also plesiomorphic, if it is accepted that the general tendency in the subtribe has been for the number of tufted segments to increase. On the other hand, the circular form of the tuft, with a raised rim, is probably an apomorphy for *R. pentacyclus*.

R. suturalis resembles *R. pentacyclus* in having a deeply impressed sutural stria and relatively limited pollinosity on the ventral surface. However, it resembles the remaining species in having the minor setae in transverse, unrimmed tufts. It is perhaps the sister species of the remaining species. It has tufts on antennal Segments V-X. The remaining species, *R. liratus*, *R. costatus*, and *R. parumcostatus* are closely related, with a very narrow sutural interval, sutural stria scarcely impressed, and ventral surface strongly pollinose. *R. parumcostatus* has tufts on Segments IV-X, in contrast to the two remaining species, which have them on Segments V-X.

KEY TO SPECIES

- 1 Minor setae in round, rimmed tufts on Segments VI-X *R. pentacyclus* new species, p. 55
- 1' Minor setae in transverse, oval tufts on Segments V-X or IV-X 2
- 2 (1') Minor setae on Segments V-X 3
- 2' Minor setae on Segments IV-X *R. parumcostatus* (Fairmaire), p. 55
- 3 (2) Sutural stria deeply impressed, coarsely punctate; lateral margin of pronotum sinuate anterior to hind angle *R. suturalis* new species, p. 59
- 3' Sutural stria very shallow, impunctate or finely, shallowly punctate; lateral margin or pronotum not sinuate anterior to hind angle 4
- 4 (3') Sutural stria pollinose, impunctate or with shallow punctures; medial margin of parasutural stria pollinose; hind calcar slightly to strongly convex dorsally *R. liratus* (Newman), p. 56
- 4' Sutural stria not impressed, represented by shallow, pollinose punctures,

not pollinose between punctures; medial margin of parasutural stria glabrous; hind calcar narrow, triangular, dorsal margin straight
 *R. costatus* (Chevrolat), p. 58

Rhyzodiastes (sensu stricto) pentacyclus new species
 (Figs. 66, 74)

Type Material.— HOLOTYPE male, labelled: "BRASILIA, Alto da Serra, Stanzel-Lachnit, CNHM-1955. Karl Brancik Colln., ex Eduard Knirsch" (AMNH). PARATYPES one male, labelled: "A. Serra, 1921" (collector's name illegible) (MZSP); two females, labelled: "Est. Biol. Boraceia, Salesópolis, São Paulo, BRAZIL, 17-10-1960, 12-V-1961, K. Lenko col." (MZSP); one male, same data as preceding but dated 17-10-1960, (MZSP); four specimens with same data as preceding but dated as follows: one male, one female 16-19-VIII-1966, Biasi, Costa & Silva (MZSP); one male, V-966, E. Rabalo (MZSP), one female, 21-22-III-1973, J. Vanin & M. Jorge, "sob a casco de tronco caído" (MZSP); two males, two females, labelled "Paranapiacaba, S. P. Brasil, 30-IX-1974, EXP. MUS. ZOOL., col tronco caído" (MZSP); one male, without locality label (MZSP).

Description.— Length 6.7-8.9 mm. Each tuft of minor setae in flat, circular space, surrounded by raised rim, present on Segments VI-X (Fig. 74); basal setae present on Segments VII-X; head short, length/greatest width 1.1; median lobe long, triangular, tip opposite posterior margin of eye, obtusely pointed; glabrous part of temporal lobe oblique, length/greatest width 4.0, glabrous area separated posteriorly from lateral margin of head by broad pollinose space, latter wider than glabrous area; eye crescentic, rather narrow; eye separated from posteriolateral angle of head by 0.3 of length of eye, medial margin of eye straight.

Pronotum short for subgenus, length/greatest width about 1.48; widest posterior to middle, base moderately narrowed; apex very strongly narrowed; lateral margins curved, base oblique on either side of midline; apex truncate; median groove narrow between median pits; anterior median pit broad; posterior median pit narrower, separated from base by 0.30 of length of pronotum; median groove posterior to it broad, containing secondary, shallower pit at base; paramedian grooves relatively narrow, sinuate; marginal groove dilated, about 0.5 as wide as outer carina at middle; inner carina sinuate, broadest posterior to middle, where three times as wide as paramedian groove; outer carina of nearly even width, widest near middle, where about 0.5 as wide as greatest width of inner carina; narrow marginal carina visible in dorsal view; prosternum with tubercle posterior to coxa.

Elytra elongate, moderately narrow; sutural stria impressed, with about 12 very coarse punctures; parasutural stria impressed, with 12-14 coarse punctures, anteriorly equal to sutural stria, posteriorly becoming slightly more dilated; intratubercular stria impressed, very coarsely punctate, abruptly narrowed opposite preapical tubercle; marginal stria impressed, coarsely punctate; punctures of all striae each about as wide as elytral interval; intervals glabrous, convex; sutural interval only slightly less convex than Interval II; latter tapered posteriorly; Interval III with apex forming preapical tubercle, latter less prominent than in other members of subgenus; apical tubercle scarcely inflated; metasternum glabrous, with median sulcus; transverse sulci of abdominal Sterna V, VI narrowly interrupted at midline, those of III, IV continuous in female, narrowly interrupted in male; male with small lateral pit on Sternum IV, female with large one; anterior femur of male with many minute round tubercles below; middle, hind tibiae with traces of tubercles; middle calcar acute, straight, very slender; hind calcar cultrate, its ventral margin raised well above bases of spurs.

The circular tufts of minor setae, with raised rims, are distinctive of this species, as is the absence of tufts from Segments IV and V. The inner pronotal carinae are broader than in other species, and the elytral intervals are nearly equal and not costate.

Variation.— The series from Salesópolis differ from the remaining specimens in having the paramedian groove closed or nearly closed anteriorly by a junction of the inner and outer carinae. The outer carinae of the pronotum also averages narrower than in the remaining localities, Alto da Serra and Paranapiacaba.

Rhyzodiastes (sensu stricto) parumcostatus (Fairmaire 1868) NEW COMBINATION
 (Fig. 68)

Rhyzodes parum-costatus Fairmaire 1868: 782.

Clinidium parumcostatum (Fairmaire) Dajoz 1975.

Rhyzodiastes parumcostatus (Fairmaire) Bell and Bell 1978.

This species was synonymized with *Clinidium costatum* (Chevrolat) by Arrow (1942), and so regarded by Hincks (1950). Dajoz (1975) recognized it as a distinct species and listed differences between it and *C. costatum*.

Type Material.— HOLOTYPE male, labelled: "Madag., *Rhysodes parumcostatum* Fairmaire" (MNHN). This must be a mislabelling, as the species is represented by numerous specimens from Brazil and one from northern Argentina, and has never been collected in Madagascar.

Description.— Length 5.6-7.7 mm. Each tuft of minor setae is oval, transverse depression, not rimmed; tufts present on Segments IV-X; basal setae present on Segments VII-X; head relatively elongate, length/greatest width about 1.23; median lobe glabrous medially, pollinose laterally, tip acute, opposite to posterior portion of eye; glabrous part of temporal lobe slightly curved, about 4.5 longer than wide; posteriolateral angle of head nearly rectangular, widely separated from glabrous part of temporal lobe; eye crescentic in lateral view; medial margin of eye slightly curved; gena with curved band of pollinosity, and diffuse pollinose area ventroposterior to it; in some specimens gena entirely pollinose.

Pronotum elongate; length/greatest width about 1.60; widest near middle; base, apex only slightly narrowed; lateral margins nearly straight, parallel, very slightly undulating; apex truncate; base strongly curved; median groove moderately broad between median pits; anterior median pit much broader than median groove; posterior median pit inconspicuous, small, separated from base by 0.3 of length of pronotum; secondary, inconspicuous posteriomedian pit at base of pronotum; median groove entirely pollinose; paramedian, marginal grooves broad, deep, pollinose; pronotal carinae largely pollinose, but each with narrow glabrous line; those of inner carinae strongly undulating; those of outer carinae nearly straight, complete (most specimens) or undulating, abbreviated posteriorly (southern specimens); marginal groove with very narrow glabrous line; prosternum without tubercle posterior to coxa.

Elytra elongate, narrow, convex; sutural stria not impressed, scarcely evident, with about 12 punctures, coarse in most specimens, in some specimens scarcely evident; parasutural stria deeply impressed, with about 12 coarse punctures; intratubercular stria impressed, coarsely punctate; marginal stria broad, shallow, scarcely impressed except near apex; parasutural stria glabrous between punctures; other striae pollinose; sutural interval flat, represented by very narrow glabrous line; Intervals II, III subcostate, largely pollinose, but with glabrous line; that of II complete; that of III complete in some specimens, limited to anterior 0.25 and preapical tubercle in others; Interval IV slightly convex, with glabrous line near humerus, latter incomplete in some specimens; preapical tubercles slightly inflated, rounded posteriorly; apical tubercles scarcely inflated; metasternum with median sulcus; metasternum largely pollinose, but with glabrous area on either side of sulcus anterior to hind coxae; transverse sulci of abdominal sterna not interrupted in midline in most specimens, in a few (both sexes) narrowly interrupted on V or VI, VI; abdominal sterna extensively pollinose, both in transverse sulci, and along posterior margin of each sternum; median longitudinal pollinose area connecting transverse sulcus with posterior margin on Sterna III, IV; male with lateral pit scarcely evident on Sternum IV; that of female deep; anterior femur of male with many minute tubercles on ventral surface; middle calcar acute, straight, very slender; hind calcar triangular, acute, moderately narrow, slightly cultrate, proximal margin convex, distal margin concave.

This species is the only member of the subgenus in which the tufts of minor setae begin on antennal Segment IV.

Range.— Southeastern Brazil and northern Argentina. We have studied the following specimens: ARGENTINA: one male, labelled: "Misiones, Dep. Concep., Sta. Maria X-1948, M. J. Viana" (MZSP). This is one of the specimens which Viana (1951) recorded as *C. costatus* Chevrolat. Viana listed two females and one additional male, and also one female from Santiago del Estero. We have not located these specimens, which were in Viana's personal collection; 19 specimens, labelled: "Rep. Arg., Misiones" without date or collector (MNHN). BRAZIL: SANTA CATARINA: three females, labelled: "Corupa (Hansa Humboldt), Nov. 1945, Dec. 1944, A. Maller coll., Frank Johnson, donor" (AMNH); one male, labelled: "Hansa, Sta. Catarina, VIII, 1910, Leudew." (MZSP); three males, labelled: "Sainte Catherine, Deyrolle 1847" (MNHN); two males, Santa Cath. (BMNH); BRAZIL, SAO PAULO, one female, labelled: "Caioba, 25-50, 48-40 (latitude, longitude), 10 m., F. Plaumann IV-1965" (MZSP); one female, labelled: "Cantareira, S.P. 20-II-1958, K. Lenko" (MZSP); two females, labelled "Ilha de Vitoria, S. Paulo 16-27 III, 1964, Exp. Dep. Zool." (MZSP); five males, ten females, labelled: "Ilha dos Buzios, S. Paulo, 16-X-4-XI 1963, Exp. Dep. Zool." (MZSP); one female, labelled: "Brasil, Cn Fairm" (GEN).

There are five additional specimens (BMNH) without precise locality data.

Variation.— The specimens from Argentina, and some of those from Santa Catarina differ from more northern specimens in having the pollinosity more extensive, with the glabrous lines of the outer carinae abbreviated posteriorly and those of Interval III obsolete except at the base and on the preapical tubercle. These might represent an additional taxon, but more specimens are required to confirm it.

Rhyzodiastes (sensu stricto) liratus (Newman 1838) NEW COMBINATION (Figs. 67, 71)

Rhysodes liratus Newman 1838: 665-666.

Clindium liratum (Newman) Fairmaire 1873b.

Rhyzodiastes liratus (Newman) Bell and Bell 1978.

Grouvelle (1903) synonymized this species with *Clinidium costatum* (Chevrolat), while Bell and Bell (1978) resurrected it.

Type Material.— LECTOTYPE (here designated) female, labelled: "*Rhysodes liratus* Newm., Rio" (BMNH). According to the original description, it was collected by Charles Darwin. PARALECTOTYPES: According to Newman, there were five specimens in the type series. We have not located any in addition to the lectotype, and do not know whether any of the paralectotypes are still preserved. Newman indicated that they were in Darwin's personal collection.

Description.— Length 6.2-7.5 mm. Each tuft of minor setae in oval transverse depression, latter not rimmed; tufts present on Segments V-X; head elongate, length/greatest width about 1.38; median lobe narrow, elongate, extending posterior to middle of eye, glabrous part of temporal lobe very narrow, elongate; pollinosity of orbital groove as broad as glabrous part of temporal lobe; posteriolateral portion of head completely pilose; eye broad, nearly semicircular in lateral view; eye separated from posteriolateral angle of head by 0.5 of length of eye; medial margin of eye curved.

Pronotum extremely elongate; length/greatest width about 1.83; base only slightly narrowed; apex moderately narrowed; lateral margins nearly straight in some specimens, slightly emarginate anterior to middle in others; base strongly curved; median groove glabrous medially, lateral slopes broadly pollinose; anterior median pit large; paramedian grooves broad, deep, largely pollinose, but with narrow glabrous area in bottom; marginal groove broad, pollinose; inner carina narrow, curved around median pits, in most specimens not broadened posteriorly, in some specimens distinctly broadened posteriorly; outer carina narrow, abbreviated posteriorly; margin with very narrow pollinose line; propleuron pollinose; prosternum pollinose except for part of intercoxal process; prosternum without postcoxal tubercle.

Elytra elongate, narrow, convex; sutural stria impunctate or faintly punctate, scarcely impressed, separated from suture by very narrow flat glabrous interval (Fig. 71), parasutural stria very deeply impressed, with 12-15 deep coarse punctures; intratubercular stria impressed, punctate, entirely pollinose; marginal stria shallowly impressed, punctate, but punctures obscured by thick pollinosity; lateral margin of Interval III pollinose; Intervals II, III, IV forming narrow glabrous carinae; preapical tubercles inflated, tapered posteriorly; apical tubercles inflated; metasternum with median sulcus; metasternum pollinose except for posterior margin, lateral borders of median sulcus; anterior part of abdomen largely pollinose; transverse sulci narrowly interrupted in midline; transverse sulci each with row of coarse punctures; female with deep lateral pit on Sternum IV; anterior femur of male with many minute tubercles on ventral surface; middle calcar acute, triangular; hind calcar with dorsal margin convex, strongly so in most specimens, only slightly so in a few specimens.

This species is most likely to be confused with *R. costatus*, which also has the tufts of minor setae beginning on Segment V, and has the sutural stria scarcely impressed. The latter species has the sutural stria punctate, with the pollinosity interrupted between the punctures. The lateral margin of Interval II is glabrous. Also, the hind calcar is triangular, with the dorsal margin not or scarcely convex, and the inner carinae of the pronotum are more broadened posteriorly.

Range.— Southeastern Brazil, north to Bahia State and south to Sao Paulo State. All localities are near to the Atlantic Coast. We have seen specimens from the following localities: BAHIA, two females, labelled: "Bahia Lewis" (BMNH), one female, two males, labelled: "Retiro, Bahia" (BMNH); two males, labelled: "Una, Bahia, Oct. 27, Friedrich" (BSL); GUANABARA (former Federal District), two females, no further data (MZSP); one female, labelled: "Corcovado 14-12-1945, Wygodzinsky" (MZSP); one male, labelled: "Corcovado, Guanabara, 700 m., Nov. 1-7, 1963, Wygodzinsky" (AMNH); one male, labelled: "Rio de J., Wygodzinsky" (BSL); RIO DE JANEIRO (STATE), one female, labelled: "Angra, E. do Rio, Pisseral. X-935, L. Tr. et Lopes" (MZSP), one female, labelled: "Floresta de DiJuca, 17-VII-1960, R. Schubartel" (MZSP); SAO PAULO: one female, labelled: "Santos, 17-23 2-99" (MNHB); one male, labelled: "Santos, 7-11-93" (MNHN); two males, one female, labelled: "Sao Paulo, J. Metz" (CNHM); STATE UNCERTAIN: one female, labelled: "Mendes, 4-IX-33, Eidmans" (BSL); one female, labelled: "P. N. do Itaiaia, 1.1958, L. C. Alvaranca" (MZSP). In addition, we have seen several specimens labelled simply "Brazil", including two members of the type series for *R. costatus* (Chevrolat) (NMW), labelled "*costatum*, Brasilia, Chevrolat".

Variation.— This species shows considerable variation in many characters, including the shape of the pronotum, the length of the marginal carina, the distinctness of the posterior median pit, and the convexity of the dorsal margin of the hind calcar. The sutural stria in most specimens is narrowly pollinose and impunctate, but in a few specimens there are indistinct punctures. The variation appears on the basis of very limited material to be geographical. The specimens from Bahia State have the posterior median pit virtually absent, the outer carina as long as the inner one, and the hind calcar less convex than in specimens from other areas. The hind calcar varies considerably within this population, in some specimens being scarcely more

convex than in *R. costatus*. The specimens from Rio de Janeiro have the posterior median pit distinct, the outer carina as in the Bahia specimens, and the hind calcar strongly convex. The specimens from Sao Paulo State have the posterior median pit distinct, the hind calcar strongly convex, and the outer carina of the pronotum abbreviated posteriorly. The available specimens are too few to be certain whether these differences represent subspecies or not. This species is in need of more detailed study.

Rhyzodiastes (sensu stricto) costatus (Chevrolat 1829)
(Figs. 70, 73)

Rhyzodes costatus Chevrolat 1829, t. 18, f. 12, in Guérin-Méneville 1829-1844.

Rhyzodes costatus (Chevrolat) Chevrolat 1844 (altered spelling of generic name).

Clinidium costatum (Chevrolat) Lewis 1888.

Rhyzodiastes costatus (Chevrolat) Bell and Bell 1978.

Type Material.—LECTOTYPE (here designated) female, labelled: "costatus, Guérin, Brasilia, Chevrolat", with red "typus" label (NMW). PARALECTOTYPES: The type series is a mixture of three species. One male and one female are *R. liratus*. One male and one female are *R. parumcostatus*. All are labelled like the lectotype, and all are in NMW. We have restricted the name to the lectotype, the one species in the series which has not been described elsewhere.

Description.—Length 6.9-7.3 mm. Each tuft of minor setae in oval transverse impression, not rimmed; tufts present on Segments V-X; head moderately elongate; length/greatest width about 1.29; median lobe narrow, elongate, extending posterior to middle of eye; glabrous portion of temporal lobe narrow, elongate; pollinosity of orbital groove as broad as glabrous portion of temporal lobe; posteriolateral portion of head completely pilose; eye broad, nearly semicircular in lateral view; eye separated from posteriolateral angle of head by 0.5 of length of eye; medial margin of eye curved.

Pronotum elongate; length/greatest width about 1.77; base only slightly narrowed; apex moderately narrowed; lateral margins slightly curved; base strongly curved; median groove broad, pollinose; paramedian grooves broad, deep, largely pollinose, but with narrow glabrous area in bottom; marginal groove broad, pollinose; inner carinae narrow, curved around anterior median pits, broader posteriorly, where distinctly broader than paramedian groove; outer carina narrow, of even width; marginal carina slightly narrower than outer carina; propleuron pollinose; prosternum pollinose except for part of intercoxal process; postcoxal tubercle absent.

Elytra elongate, narrow, convex; sutural stria not impressed, represented by row of shallow pollinose punctures, pollinosity absent between punctures except in some specimens, where present in posterior 0.25 of stria (Fig. 73); parasutural stria impressed, punctured, medial margin glabrous, lateral margin pollinose; intratubercular stria deeply impressed, pollinose; marginal stria shallowly impressed, punctures obscured by thick pollinosity; Interval II only moderately convex; Intervals III, IV forming narrow, glabrous carinae; preapical tubercles scarcely inflated posteriorly; apical tubercles slightly inflated; metasternum with median sulcus; metasternum very finely pollinose or microsculptured; abdominal sterna dull, very finely pollinose or microsculptured; transverse sulci narrowly interrupted in midline, each with pit at medial end, otherwise impunctate or obscurely punctate; female with deep lateral pit on Sternum IV; anterior femur of male with many minute tubercles on ventral surface; middle calcar acute, triangular; hind calcar narrow, acute, distinctly proximad to tibial spurs.

This species differs from *R. liratus* in having the sutural stria represented by a row of isolated punctures, these not connected by pollinosity except near elytral apex, in lacking pollinosity on the medial margin of the parasutural stria (in other words, on the lateral margin of the second interval), and in having the hind calcar narrowly triangular with the dorsal margin straight.

Range.—Southern Brazil, except for one female, labelled: "Rio Jano., FRY" (BMNH), from more inland localities than *R. liratus*. We have seen one male and three females, labelled "Matto Grosso, de Castelnau, 12-47" (MNHN), and one male, labelled: "Vicosia, M. G., 23-7-57, coll. J. Becker" (MZSP). "M.G." indicated Minas Gerais State. The characters of this species are approached by some of the variants of *R. liratus*, and it is possible that the two are only subspecifically distinct. However, the presence of both forms at Rio de Janeiro makes this doubtful. Like *R. liratus*, this form needs more study.

Rhyzodiastes (sensu stricto) suturalis new species
(Figs. 69, 72)

Type Material.— HOLOTYPE female, labelled: "Espiritu Santo, Sooretama, Linhares, X. 962, Pereira, Alv. Martins" (MZSP).

Description.— Length 7.4 mm. Each tuft of minor setae in oval transverse depression, not rimmed; tufts present on Segments V-X; head elongate, length 1.33 times greatest width; median lobe narrow, elongate, extending posterior to middle of eye, glabrous part of median lobe narrow, only slightly broader than pollinosity of orbital groove; posteriolateral portion of head completely pilose; eye broad, nearly semicircular in lateral view; medial margin of eye curved; eye separated from posterior angle of head by 0.5 of length of eye.

Pronotum elongate; length/greatest width 1.71; base, apex slightly narrowed; lateral margin with long, shallow sinuation anterior to hind angle; base strongly curved; median groove broad, bottom glabrous, margins pollinose; paramedian grooves broad, deep, pollinose; marginal groove moderately broad, pollinose, abbreviated anterior to sinuation of lateral margin; inner carinae narrow, convex, curved around anterior median pit; outer carina narrow, convex, complete; marginal carina complete; base of pronotum narrowly margined with pollinosity; propleuron largely glabrous, but very finely pollinose or microsculptured near notopleural suture; prosternum glabrous; postcoxal tubercle absent.

Elytra moderately narrow, elongate, but broader than in *R. liratus*, humeri strongly narrowed; sutural stria deeply impressed, with about 11 coarse punctures, bottom glabrous, margins pollinose; parasutural stria deeply impressed, becoming broader posteriorly, with about 12 coarse punctures; parasutural stria glabrous, lateral margin pollinose, medial margin nearly glabrous, with trace of pollinosity posteriorly; intratubercular stria impressed, broad, coarsely punctate, punctures obscured by pollinosity; marginal stria narrow, impressed, pollinose; sutural interval broad, convex, wider than second interval, glabrous; second interval convex, posterior 0.5 subcarinate; third interval narrow convex, fourth interval nearly flat; preapical tubercle strongly inflated, apex tapered; apical tubercle inflated; metasternum with median sulcus, largely glabrous; abdominal sterna largely glabrous; transverse sulci narrowly interrupted in midline, with enlarged pits at medial ends, coarsely punctate, narrowly pollinose; female with round lateral pit in Sternum IV; male unknown.

This species resembles *R. liratus* and *R. costatus* in having the minor setae in oval tufts on Segments V-X. It differs from them in having the sutural stria very strongly impressed and coarsely punctate and in the shape of the pronotum. The deep sutural stria gives it the appearance of *R. pentacyclus*. The latter species, however, has the minor setae in circular, rimmed tufts on Segments VI-X.

GENUS *CLINIDIUM* KIRBY 1835

Description.— Part I: 62

KEY TO SUBGENERA (slightly revised from Part I: 62)

- | | | |
|--------|--|----|
| 1 | Cleaning organ of anterior tibia entirely proximad to basal articulation of anterior tarsus | 2 |
| 1' | Cleaning organ more distad, basal articulation of tarsus opposite its midpoint | 4 |
| 2 (1) | Tufts of minor setae present on Antennal Segments VII-X; pronotum widest near middle; angular seta present; marginal setae absent; intercalary stria ending blindly posteriorly, except in <i>C. halffteri</i> and some <i>C. guatemalenum</i> | 60 |
| 2' | Tufts of minor setae present on antennal Segments VI-X; pronotum widest distinctly behind middle; either both angular, marginal setae present, or else both absent; intercalary stria not ending blindly posteriorly | 3 |
| 3 (2') | Parasutural stria complete anteriorly, reaching base of elytron; pronotum without setae | 69 |
| 3' | Parasutural stria restricted to posterior 0.5 to 0.25 of elytron; pronotum | |
- Mexiclinidium* Bell and Bell, p. 60
Protainoa Bell and Bell, p. 69

- with marginal, angular setae *Tainoa* Bell and Bell, p. 70
- 4 (1') Marginal stria clearly sixth from suture; all striae well developed; inner elytral intervals carinate, marginal groove of pronotum double or single *Arctoclinidium* Bell, p. 75
- 4' Striation more reduced; marginal stria fourth or fifth from suture; supramarginal stria absent; inner elytral intervals not carinate or scarcely so; marginal groove of pronotum single *Clinidium sensu stricto*, p. 93

SUBGENUS *MEXICLINIDIUM* BELL AND BELL 1978

Type species.— *Clinidium mexicanum* Chevrolat 1873a.

Description.— Antenna with tufts of minor setae on Segments VII-X; antennal stylet small; 1 temporal seta present; eye narrowly crescentic (narrower than in *Arctoclinidium*); orbital groove pollinose, complete, reaching posterior margin of temporal lobe; pronotum with lateral margins curved, marginal groove double or single; pronotum with angular setae (except for *newtoni*), but without marginal setae; sternopleural grooves absent; elytral striae complete; marginal stria fifth or sixth from suture; supramarginal stria impressed in most specimens, represented by row of punctures in some specimens, absent in *C. championi*; intercalary stria ending blindly anterior to preapical tubercle, except in *C. halfferi* and some specimens of *C. guatemalenum*; intervals of elytra elevated, costate in most species; elytral setae more numerous than in *Arctoclinidium*; metasternum without median sulcus; female with enlarged lateral pit in Sternum IV; female without elytral cauda; anterior femur of male with ventral tooth; anterior tibia of male with proximal tooth present or absent; base of anterior tarsus entirely distad to cleaning organ; calcars small, hind calcar smaller than middle calcar.

The deep elytral striae and carinate intervals make most members of this subgenus superficially similar to *Arctoclinidium*. The position of the cleaning organ and the more numerous elytral setae separate it from the latter subgenus. Most *Mexiclinidium* differ from *Arctoclinidium* in the anastomosis of Intervals III and IV posterior to the end of the intercalary stria. In *C. halfferi* and some specimens of *C. guatemalenum*, the intercalary stria is complete and the intervals do not anastomose.

Mexiclinidium is known from central and southern Mexico and from Guatemala.

Phylogeny.— The nine species can be grouped as follows:

- I. *mexicanum* group
 - C. mexicanum*
 - C. balli*
 - C. triplehorni*
- II. *blomi* group
 - C. blomi*
 - C. iviei*
- III. *guatemalenum* group
 - C. guatemalenum*
 - C. newtoni*
- IV. *championi* group
 - C. championi*
 - C. halfferi*

The *mexicanum* group contains three very similar species which differ mainly in secondary sexual characters. The group occupies a compact area on the Mexican Plateau and its eastern margin. The outer marginal groove of the pronotum is shallow or absent, the transverse sulci of the abdomen are deep and widely separated, elytral setae are few, the male first trochanter is toothed, and Sternum VI has many round punctures.

The *blomi* group has two species, one on either side of the gap in the mountain chain at Tehuantepec. These have the outer marginal groove deep but hidden in dorsal view, the transverse sulci deep and widely separated, the male first trochanter toothed. Elytral setae are many, and Sternum VI either has elongate punctures (*iviei*) or else two pairs of impressions (*blomi*).

The *guatemalenum* group has two species in the highlands of Chiapas and Guatemala. They have a pair of precoxal setae. The outer marginal groove is deep and is visible in dorsal view. The median lobe of the head is shorter than in the two preceding groups. The transverse sulci of the abdomen are deep and are only narrowly separated medially. Elytral setae are few. The male first trochanter is toothed (*newtoni*) or rounded (*guatemalenum*). Sternum VI is coarsely punctate.

The *championi* group has two species, one in the Quiche Mountains of Guatemala, the other from a relatively low elevation near the Gulf of Mexico. These species have Sternum VI with a narrow submarginal groove and a pair of pits near the base. The first trochanter of the male is rounded, and the transverse sulci of the abdomen are relatively shallow. Otherwise the two species are quite dissimilar, and perhaps are not closely related. *C. championi* has the median lobe of the head elongate, the outer marginal groove of the pronotum deep and visible in dorsal view (as in the *guatemalenum* group), and the elytral setae few. *C. halffteri* has the median lobe short and truncate, the outer marginal groove absent, and the elytral setae numerous.

KEY TO SPECIES

- | | | |
|----|---|---|
| 1 | Outer marginal groove of pronotum visible in dorsal view | 2 |
| 1' | Outer marginal groove of pronotum not visible in dorsal view | 4 |
| 2 | Transverse sulci of abdomen present, pilose; Sternum VI coarsely punctured, submarginal sulcus absent | 3 |
| 2' | Transverse sulci of abdomen absent, represented by isolated punctures; Sternum VI with crescent-shaped submarginal sulcus | |
| | <i>C. championi</i> new species, p. 62 | |
| 3 | Apex of pronotum narrowed, evenly curved; postorbital, suborbital tubercle present; medial ends of transverse sulci without enlarged pits | |
| | <i>C. newtoni</i> new species, p. 63 | |
| 3' | Apex of pronotum truncate; postorbital, suborbital tubercle absent; medial ends of transverse sulci with enlarged pits | |
| | <i>C. guatemalenum</i> Sharp, p. 63 | |
| 4 | Intercalary stria ending blindly posteriorly; Intervals III, IV anastomosing posteriorly; median lobe of head elongate, tip acute, opposite or behind posterior region of eye | 5 |
| 4' | Intercalary stria complete; Intervals III, IV not anastomosing; median lobe of head short, tip truncate, opposite middle of eye | |
| | <i>C. halffteri</i> new species, p. 66 | |
| 5 | Sternum VI with a pair of median pilose, oval impressions | |
| | <i>C. blomi</i> Bell, p. 66 | |
| 5' | Sternum VI with scattered, round or elongate punctures | 6 |
| 6 | Punctures of Sternum VI elongate, coalesced; Sternum VI impressed | |
| | <i>C. iviei</i> new species, p. 69 | |

6'	Punctures of Sternum VI large, round; Sternum VI unimpressed	7
7	Calcars present, males	8
7'	Calcars absent, females	10
8	Proximal tooth of anterior tibia present	9
8'	Proximal tooth of anterior tibia absent	
 <i>C. triplehorni</i> new species, p. 68	
9	Proximal tooth of anterior tibia large; femoral tooth large, almost carinate	
 <i>C. mexicanum</i> Chevrolat, p. 67	
9'	Proximal tooth of anterior tibia small, oblique; femoral tooth small, oblique	
 <i>C. balli</i> new species, p. 68	
10	Lateral pit of Sternum IV glabrous	11
10'	Lateral pit of Sternum IV pollinose <i>C. triplehorni</i> new species, p. 68
11	Basal impressions of pronotum relatively large, 0.25 of length of pronotum; supramarginal stria impressed or represented by coarse punctures	
 <i>C. mexicanum</i> Chevrolat, p. 67	
11'	Basal impressions small, less than 0.20 of length of pronotum; supramarginal stria not impressed, represented by fine punctures	
 <i>C. balli</i> new species, p. 68	

Clinidium (Mexiclinidium) championi new species

(Figs. 75, 98)

Type Material.— HOLOTYPE male, labelled: "Quiche Mountains, 7-9000 ft., Champion" (BMNH). This locality is in Guatemala near Totonicapan.

Description.— Length 6.0 mm. Head as broad as long; median lobe long, tip opposite posterior margin of eye; medial margin of temporal lobe nearly straight.

Pronotum relatively short; length/greatest width 1.30; lateral margin moderately curved; base slightly narrowed, apex moderately narrowed; basal impression relatively large, length 0.33 of length of pronotum; basal impression closed posteriorly; inner, outer marginal grooves equally deep, outer marginal groove conspicuous in dorsal view; marginal carina curved, narrow; prosternum without precoxal seta on each side.

Striae impressed, coarsely punctured, narrowly pollinose; intervals convex, but not distinctly costate; supramarginal stria absent; sutural stria with one seta near apex; intercalary stria with two setae in apical 0.33; intratubercular stria without setae; marginal stria with five setae near apex; transverse sulci broadly interrupted in midline, scarcely impressed, not pollinose, each represented by row of punctures; male with small pollinose lateral pit on Sternum IV; Sternum VI with small round pit near each anteriolateral angle, curved submarginal groove (Fig. 98); male with small obtuse ventral tooth on anterior femur; male with anterior trochanter rounded; anterior tibia of male without proximal tooth; middle calcar triangular, acute, base relatively broad; hind calcar small, triangular, apex acute, distal margin raised well above level of spurs; female unknown.

This species differs from all others in the subgenus except *C. halfpteri* in having the striae shallower and the inner intervals not truly costate. The reduction of the transverse sulci to rows of punctures is also distinctive. The absence of precoxal setae and impunctate sixth sternum easily separate it from the sympatric *C. guatemalenum*. *C. halfpteri* differs in lacking the outer marginal groove and in having the supramarginal stria impressed.

We have named this species for the collector, George Champion, who collected fine series of Rhyssodidae in Central America.

Clinidium (Mexiclinidium) newtoni new species

(Figs. 77, 86)

Type Material.— HOLOTYPE male, labelled: "MEXICO, Chiapas, 8 mi. N. Pueblo Nuevo S., 6000', cl. for. 26-27 VIII-73, N. 541 A. Newton" (BSRI).

Description.— Length 7.0 mm. Head slightly longer than broad; median lobe long, ended just anterior to posterior margin of compound eye; frontal grooves relatively shallow, convergent posteriorly; medial margins of temporal lobes oblique, convergent posteriorly; small postorbital, suborbital tubercles present.

Pronotum relatively short; length/greatest width 1.40; lateral margins curved; apex strongly narrowed; base moderately narrowed; basal impression large, 0.3 of length of pronotum; basal impression open posteriorly; inner, outer marginal grooves equally deep, outer marginal groove conspicuous in dorsal view; marginal carina curved, narrow; prosternum with precoxal setae; angular seta apparently absent.

All striae, including supramarginal deeply impressed; sutural stria with one or two setae near apex; intercalary stria without setae; intratubercular stria with two setae near apex; transverse sulci of abdominal sterna narrowly interrupted in midline, medial ends of sulci not enlarged; Sternum VI with a few very coarse punctures; anterior femur of male with very prominent ventral tooth, latter truncate with apex in form of oblique ridge; anterior trochanter of male with obtuse ventral tooth; male anterior tibia without proximal tooth, posterior face of anterior tibia with conical tooth opposite middle of cleaning organ (Fig. 86); middle calcar small, acute; hind calcar larger, dorsal margin emarginate near base (calcar thus slightly falcate); female unknown.

The distinct postorbital and suborbital tubercles of this species are unique within the subgenus. The presence of precoxal setae and the narrow interruption of the transverse sulci of the sterna are points of similarity to *C. guatemalenum*, but the latter species has enlarged pits at the medial ends of the transverse sulci, and the pronotum is much less narrowed and rounded anteriorly. *C. blomi*, which is probably sympatric with *C. newtoni*, differs in having the transverse sulci broadly interrupted, the precoxal setae absent, the pronotum much less narrowed anteriorly, and in numerous secondary characters of the male.

The species is named in honor of the collector, Alfred F. Newton, Jr.

Clinidium (Mexiclinidium) guatemalenum Sharp 1899

(Figs. 76, 101)

Clinidium guatemalenum Sharp 1899: 489.

Clinidium (Arctoclinidium) guatemalenum (Sharp) Bell 1970.

Clinidium (Mexiclinidium) guatemalenum (Sharp) Bell and Bell 1978.

Type Material.— LECTOTYPE (here designated) male, labelled: "GUATEMALA, San Geronimo, Vera Paz Prov., coll. Champion" (BMNH). PARALECTOTYPES one male, three females, same data as lectotype (BMNH).

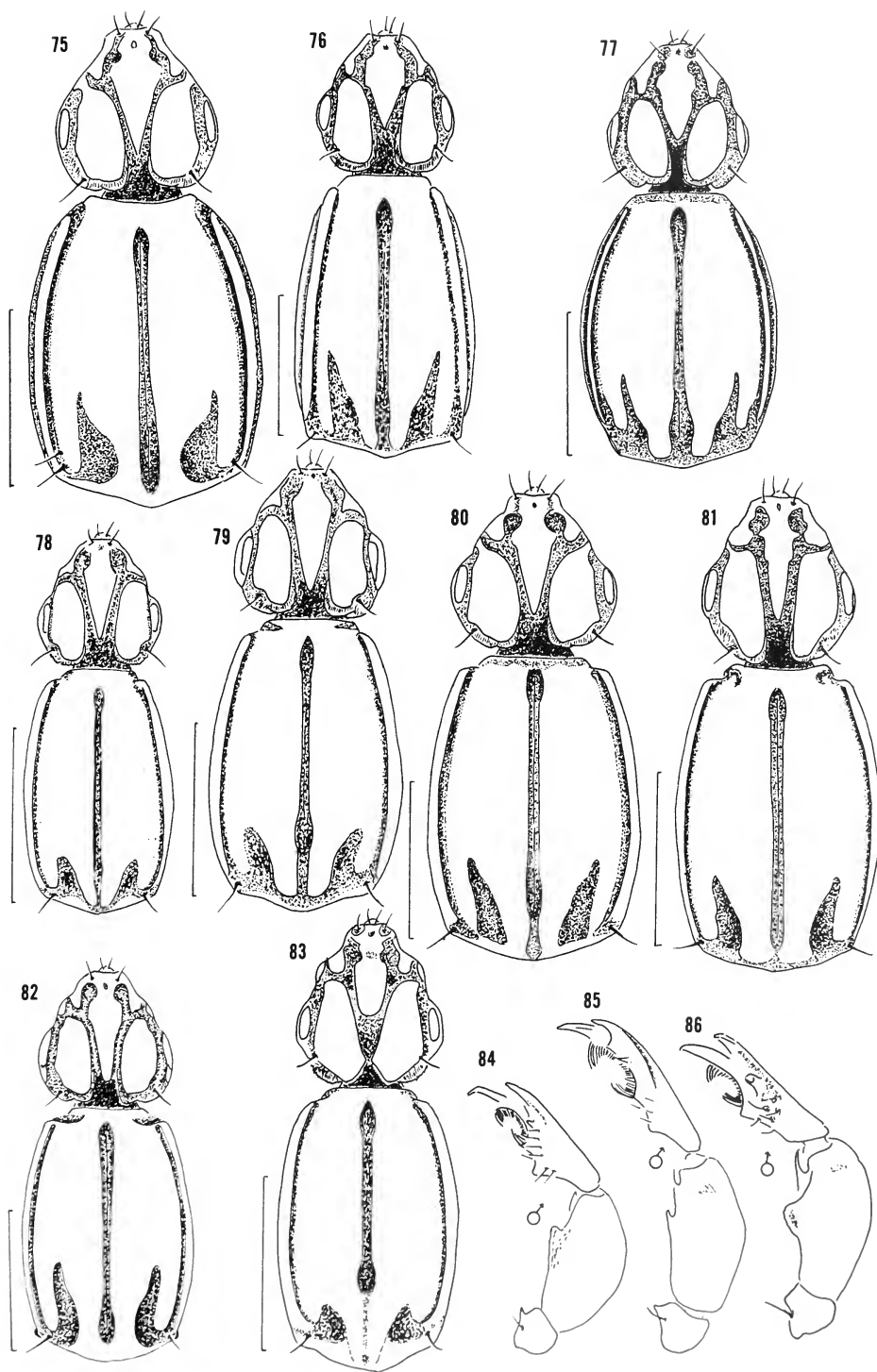
Description.— Length 7.0-7.7 mm. Head longer than broad; median lobe short, tip opposite middle of eye; medial margin of temporal lobe curved.

Pronotum relatively elongate, length/greatest width 1.48; lateral margins curved; apex strongly narrowed, basal margin moderately narrowed; basal impression relatively large, 0.4 of length of pronotum; basal impression closed posteriorly, closed or open laterally; inner, outer marginal grooves equally deep, outer marginal groove conspicuous in dorsal view; marginal carina curved, narrow; prosternum with precoxal seta on each side.

All striae, including supramarginal deeply impressed; sutural stria with one or two setae near apex; intercalary stria with two or three setae in posterior 0.5; intratubercular stria with two or three setae in posterior 0.3; marginal stria with three to five setae near apex; transverse sulci of abdominal sterna very narrowly interrupted in midline, medial end of each sulcus with enlarged pit; Sternum VI coarsely punctate (Fig. 101); lateral pit of Sternum IV in female glabrous; anterior femur of male, with acute, narrow, ventral tooth with one seta; male with anterior trochanter rounded; male anterior tibia with large proximal tooth; middle calcar triangular, acute, base relatively broad; distal margin not elevated above spurs; hind calcar small, triangular, apex acute, distal margin elevated above level of spurs; female without ventral tooth on anterior femur.

In the form of the pronotum, this species is closest to *C. blomi*, but the coarsely punctate Sternum VI separates it from the latter species, and the closely approximate medial pits on the transverse sulci are unique within the subgenus. The presence of precoxal setae is shared only with *C. newtoni*. The latter species differs in male secondary sexual characters and in the

Plate 7. Figs. 75–86. Genus *Clinidium*, Subgenus *Mexiclinidium*. Figs. 75–83, Head and pronotum, dorsal aspect; Fig. 75, *C. (M.) championi* new species; Fig. 76, *C. (M.) guatemalenum* Sharp; Fig. 77, *C. (M.) newtoni* new species; Fig. 78, *C. (M.) balli* new species; Fig. 79, *C. (M.) triplehorni* new species; Fig. 80, *C. (M.) blomi* Bell; Fig. 81, *C. (M.) mexicanum* Chevrolat; Fig. 82, *C. (M.) iviei* new species; Fig. 83, *C. (M.) halffteri* new species; Figs. 84–86, Anterior leg, male (excluding tarsus); Fig. 84, *C. (M.) iviei* new species; Fig. 85, *C. (M.) balli* new species; Fig. 86, *C. (M.) newtoni* new species.



absence of pits at the medial ends of transverse sulci and in the presence of postorbital and suborbital tubercles.

Range.— Guatemala. In addition to the type series we have studied the following specimens: two males, two females, labelled: "Chichivac, Chimaltenango Prov., 8600', Aug. 19, 1926, J. R. Slevin" (CAS); two females, labelled: "El Quiche, 7.3 km from Chichicastenango, 14° 54' N, 91° 07' W, 2400 m., May 28, 1973, T. L. & L. J. Erwin" (NMNH); one male, one female, labelled: "Quiche Mts., 8500-10500 ft., Tonicapam, coll. Champion" (BMNH).

In the type series, the parasutural stria is interrupted for a short distance just anterior to the apex of the intercalary stria, so that a narrow bridge connects Intervals II and III.

In the specimens from other localities, this is not true. The specimens from Chichivac have a shallow median impression on the metasternum, though it does not form a discrete sulcus. There is no trace of this impression in the type series. It is not certain whether these variations are individual differences or represent geographic variation.

Clinidium (Mexiclinidium) blomi Bell 1970
(Fig. 80)

Clinidium (Arctoclinidium) blomi Bell 1970: 309.

Clinidium (Mexiclinidium) blomi (Bell) Bell and Bell 1978.

Type Material.— HOLOTYPE MCZ 31747, male, labelled: "Rancho Nuevo 8 1/2 miles SE of San Cristobal de las Casas, Chiapas, Mexico, coll. R. T. Bell, D. H. Van Horn, July 23, 1956" (MCZ). PARATYPES, three females collected with the type (UVM); four males, eight females, collected at same locality, Sept. 1, 1967, by Ball, Erwin, and Leech (ALB).

Description.— Length 6.1-7.5 mm. Head nearly as broad as long; median lobe long, tip posterior to hind margin of eye; medial margin of temporal lobe curved.

Pronotum relatively short; length/greatest width about 1.40; lateral margins curved; apex strongly narrowed; base moderately narrowed; basal impression about 0.3 of length of pronotum; basal impression closed posteriorly, laterally; inner, outer marginal grooves equally deep; outer groove placed more laterally than in *C. guatemalenum*, scarcely visible in dorsal view; marginal carina curved, conspicuous; prosternum without precoxal setae.

All striae, including supramarginal, deeply impressed; sutural stria with two to four setae, most anterior of them anterior to middle of stria in most specimens; intercalary stria with complete row of five setae, most anterior of them near to elytral base; intratubercular stria with two or three setae near apex; marginal stria with five or six setae in apical 0.5; transverse sulci of abdominal sterna broadly interrupted in midline, without medial pits; Sternum VI not punctate, but with two pairs of oblique impressions; lateral pits of Sternum IV of female pollinose; anterior femur of male with large, broad ventral tooth with one seta; anterior trochanter of male dentate; anterior tibia of male with large proximal tooth; middle calcar acute, base narrow, not elevated above spurs; hind calcar small, triangular, apex acute; distal margin elevated above level of spurs; female with anterior femur not dentate.

This species resembles *C. guatemalenum* in having inner and outer marginal grooves of the pronotum equally developed, separated by a narrow marginal carina. In this species, however, the marginal carina is directed more laterally than in *C. guatemalenum* so that the outer groove is almost hidden in dorsal view. Unique to *C. blomi* are the great development of the elytral setae and the absence of coarse punctures on Sternum VI.

Range.— High Plateau of Chiapas, southeastern Mexico. In addition to the type material we have seen one specimen labelled: "Mexico: 5 mi. w. of San Cristobal, 7500', V-23-1961, J. M. Campbell" (BSRI).

Clinidium (Mexiclinidium) halffteri new species
(Figs. 83, 99)

Type Material.— HOLOTYPE male, labelled: "MEXICO, Ver., Amates, 29-V-1964, Catemaco, Halffter, Reyes" (MZSP). PARATYPES two males, same label as holotype (MZSP). The type locality is in southern Vera Cruz State, near the Gulf of Mexico, at a low elevation.

Description.—Length 6.1–6.5 mm. Head slightly longer than broad; median lobe short, tip subtruncate, opposite middle of eye; frontal grooves very narrow; frontal space very small; medial margins of temporal lobes convergent to narrowly separated medial angles, latter posterior to hind margin of eye; posteriomarginal margin oblique.

Pronotum rather elongate; length/greatest width 1.58; lateral margins weakly curved; apex less narrowed than base; basal impressions very small, 0.12 of length of pronotum, closed posteriorly; outer marginal groove entirely absent; prosternum without precoxal setae.

Elytra much broader than pronotum; margins parallel for most of length; humeri strongly, obliquely narrowed; elytral intervals convex, inner ones not carinate; intercalary stria complete; Intervals III, IV not anastomosing posteriorly; intratubercular stria impressed at base, apex; middle portion not impressed, represented by row of coarse punctures; supramarginal stria not impressed; represented by row of punctures very close to those of intratubercular stria in middle 0.33; base, apex absent; marginal stria with base, apex impressed, middle 0.33 represented by row of punctures; sutural stria with two setae near apex; parasutural stria with four or five setae in apical 0.5; intercalary stria with complete row of five or six setae; intratubercular stria with one seta near apex; marginal stria with four or five setae in apical 0.33; transverse sulci of abdomen narrow, each with row of coarse punctures, broadly interrupted in midline; without enlarged punctures at medial end; Sternum VI of abdomen with small pit near each anteriolateral angle, long submarginal groove, its end angled medially (Fig. 99); anterior femur of male with large, sharp ventral tooth, without setae; anterior trochanter of male rounded; anterior tibia of male without proximal tooth; middle calcar slender, rather long, apex obtuse; hind calcar triangular, apex obtuse, only slightly elevated above level of spurs; female unknown.

This species is distinguished from all other members of the subgenus in having the median lobe short and truncate, and the temporal lobe with distinct medial angles. The pronotum is also distinctive, with the base slightly more narrowed than the apex and the outer marginal groove entirely absent. It is the only member of the subgenus to have setae in the parasutural stria.

The species is named for the collector, Dr. Gonzalo Halffter, a skilled specialist in Scarabaeidae and insect behavior.

Clinidium (Mexiclinidium) mexicanum Chevrolat 1873a
(Figs. 81, 100)

Clinidium mexicanum Chevrolat 1873a: 214.

Clinidium (Arctoclinidium) mexicanum (Chevrolat) Bell 1970.

Clinidium (Mexiclinidium) mexicanum (Chevrolat) Bell and Bell 1978.

Type Material.—According to the original description, there is a type series of seven specimens, collected in May, 1855 by Agusté Sallé, under pine bark at Jacale, at the Park of Orizaba. We have studied one male and one female of this series, labelled: "Jacale, Mexico, Sallé coll." (BMNH). Both are labelled as cotypes. We have not located the other five specimens. The pair which we have studied fit the concept of *C. mexicanum* of previous authors in all respects except one; both specimens are virtually without the outer marginal groove of the pronotum. This is probably an individual variation, as we have seen a few specimens from other localities which have the groove strongly reduced. Nevertheless, there might be two taxa in the type series, so we feel it improper to designate a lectotype until we have seen the rest of the series.

Description.—Length 6.0–8.5 mm. Head slightly longer than broad; median lobe long, tip posterior to hind margin of eye; medial margins of temporal lobes nearly straight, nearly parallel.

Pronotum relatively elongate; length/greatest width about 1.47; lateral margins curved, apex strongly narrowed; base moderately narrowed; basal impressions small, less than 0.25 of length of pronotum, open posteriorly; outer marginal groove completely hidden in dorsal view, shallower than inner marginal groove, fine but complete in most specimens, effaced anteriorly in a few specimens, nearly absent in a few specimens; prosternum without precoxal setae.

Supramarginal stria shallow in most specimens, in some specimens not impressed, represented by row of coarse punctures; remaining striae impressed; sutural stria with two or three setae near apex; intercalary stria with two or three setae posterior to middle; intratubercular stria with two or three setae posterior to junction with supramarginal; marginal stria with five or six setae near apex; transverse sulci of abdomen broadly interrupted in midline, without pits at medial ends; Sternum VI of abdomen coarsely punctate (Fig. 100); lateral pit of Sternum IV in female glabrous; anterior femur of male with large, sharp ventral tooth with several setae; anterior trochanter of male dentate; anterior tibia of male with large proximal tooth; middle calcar acute, base moderately broad, elevated above level of spurs; hind calcar small, less acute than in *C. blomi*, base broad, elevated well above level of spurs.

This species is most easily separated from *C. triplehorni* and *C. balli* by the secondary sexual characters of the male. It is also larger than the two related species, and has the

supramarginal stria better developed.

Range.— Mountains of the southern end of the Mexican Plateau, from Jalisco to Vera Cruz State, from 5000 to 12,000 feet elevation. Bell (1970) gives a list of localities. We have seen specimens from the following additional localities. MEXICO STATE: Temescaltepec, long series of both sexes, coll. Hinton, Usinger (BMNH) (this locality is near to Tejupilco des Hidalgo); four males, four females 18 km. SW of Toluca, meadow, 3400 m., April 22, 1977, coll. J. S. Ashe, H. E. Frania, D. Shepley (ALB); MORELOS: one female, 7 mi. s. of Tres Cumbres, VII-7, 1975, coll. Triplehorn (OSU); PUEBLA, one male, one female, 50.8 km. se of Azuabilla, 2480 m., oak pine forest, logs, ground, 78B-36a, Dec. 24-25, 1978, G.E., K. E. Ball (ALB); six males, nine females, 37.5 km. se of Azuabilla, 2500 m., wet oak-pine, 78B-37, G.E., K.E. Ball (ALB); one female, 7.6 km. e. of Santa Maria del Monte, wet pine-oak forest, 2480 m., VII-9-1975, G. E. Ball, H. E. Frania (ALB). These new records do not significantly extend the range of the species.

Variation.— The most significant variation is in the development of the outer marginal groove of the pronotum. In a large majority of specimens, it is complete. In a few, the anterior part is effaced, and in the two cotypes studied by us, it is entirely effaced, as in *C. balli* and *C. triplehorni*. It appears to us that this is an individual aberration, without taxonomic importance, though its presence in both the cotypes is surprising.

Clinidium (Mexiclinidium) balli new species
(Figs. 78, 85, 97)

Type Material.— HOLOTYPE male, labelled: "G. Ball Colln., MEXICO: Hgo, 16 mi. N. Zimapan 8000', at night, V-27-1974, C. & L. O'Brien & Marshall" (NMNH). PARATYPES two males, one female, same data as type (NMNH); three males, two females, labelled: "MEX:S. Luis Potosi, 14 mi. W. Xilitla, 4800'; VI-29-73, A. Newton" (MCZ); one male labelled: "MEX, Hidalgo, 4 mi. S.W. Chapalhuacan, 3500', VII-5-1976, A. Newton" (MCZ).

Description.— Length 5.0-6.0 mm. Head slightly longer than broad; median lobe not quite so long as in *C. mexicanum*, tip even with posterior margin of eye, blunter than in *C. mexicanum*; medial margins straight, parallel.

Pronotum elongate; length/greatest width 1.54; lateral margins curved; apex slightly more narrowed than base; basal impression very small, about 0.15 of length of pronotum, open posteriorly; outer marginal groove almost absent, less than 0.1 of length of pronotum, ventrad to hind angle; prosternum without precoxal setae.

Supramarginal stria not impressed, represented by row of fine punctures; marginal stria impressed at apex, represented at middle by row of fine punctures; both marginal, supramarginal striae with anterior 0.33 entirely effaced; sutural stria with one seta near apex; intercalary stria with one seta near apex; intratubercular stria without setae; marginal stria with three or four setae near apex; transverse sulci of abdomen broadly interrupted at midline, without pits at medial ends; Sternum VI of abdomen coarsely punctate; lateral pit of Sternum IV in female glabrous (Fig. 97); anterior femur of male with small, oblique ventral tooth, without setae; anterior trochanter of male dentate; anterior tibia of male with small, obtuse proximal tooth; middle calcar acute, base narrow, not raised above level of spurs; hind calcar small, base broad, scarcely raised above level of spurs.

This species is close to *C. mexicanum*, but has the supramarginal and marginal striae effaced anteriorly. The males is easily recognized by the small proximal tooth on the anterior tibia and the oblique tooth on the anterior femur (Fig. 85). *C. triplehorni* has the proximal tooth entirely lacking.

We take pleasure in naming this species for our longtime friend, Dr. George Ball, who has made long series of Mexican *Clinidium* available to us.

Clinidium (Mexiclinidium) triplehorni new species
(Figs. 79, 96)

Type Material.— HOLOTYPE male, labelled: "MEXICO, Hgo. 7 mi. ne. of Jacala, VI-23-1975, C. A., W. E., B. W. Triplehorn" (OSU). According to Dr. Triplehorn (*in litt.*), the elevation of the type locality is about 3200'. Despite the similar spelling, this locality is not the same as Jacale, the type locality for *C. mexicanum*. PARATYPES four males, two females, same label as holotype (OSU).

Description.— Length 6.0-6.7 mm. Head slightly longer than broad; median lobe long, tip posterior to hind margin of eye, blunter than in *C. mexicanum*; medial margins of temporal lobes straight, nearly parallel.

Pronotum elongate, length/greatest width 1.54; lateral margins curved; apex strongly narrowed; base moderately narrowed; basal impression small, about 0.2 of length of pronotum, open posteriorly; outer marginal groove reduced to 0.2 of length of pronotum, ventrad to hind angle; prosternum without precoxal setae.

Supramarginal stria not impressed, represented by row of very fine punctures; marginal stria impressed near apex, base, otherwise represented by row of fine punctures; sutural stria without setae or with one near apex; intercalary stria without setae or with one or two near apex; intratubercular with one seta near apex; marginal stria with three or four near apex; transverse sulci of abdomen broadly interrupted in midline, without pits at medial ends; Sternum VI of abdomen coarsely punctate; lateral pit of Sternum IV in female pollinose (Fig. 96); femur of male with very small obtuse ventral tooth, without setae; anterior trochanter of male dentate; anterior tibia of male without proximal tooth; middle calcar acute, base broad, not raised above level of spurs; hind calcar small, acute, base narrow, raised well above level of spurs.

This species resembles *C. mexicanum*, but differs strongly in secondary sexual characters, entirely lacking the proximal tooth on the anterior tibia in the male. The female, unlike *C. mexicanum* and *C. balli*, has the lateral pit of Sternum IV pollinose.

We dedicate this species to the collector, Dr. Charles Triplehorn, in appreciation of his making the type series and other Mexican Rhysodini available for study.

Clinidium (Mexiclinidium) iviei new species

(Figs. 82, 84, 102)

Type Material.— HOLOTYPE male, labelled: "MEX: Oaxaca, 2 mi. S. Cerro Pelon, 03 Jul 1982, 8-9000 ft. M. A. Ivie Coll., ex rotten pine" (NMNH). PARATYPES two males, eight females, same data as holotype (NMNH); one male, one female each (UCD, UVM, MAI). All forementioned paratypes with same data as holotype; one male, two females (UVM); one male, one female (OSU); one male, one female (R. S. Miller Colln.); one male, one female sent to Thomas Atkinson at the Colegio de Post-graduados, Chapingo, Mexico. All forementioned paratypes with same locality data as holotype but labelled "July 2, 1982, (R. S. Miller Coll.)"; one female, labelled "Mexico, Oaxaca, 28 mi. N. Ixtlán de J., 10,000', VII-23-29, 1971, A. Newton, under pine bark (MCZ).

Description.— Length 6.2-8.0 mm. Head slightly longer than broad; median lobe long, tip posterior to hind margin of eye; medial margins of temporal lobes slightly curved.

Pronotum relatively elongate, length/greatest width 1.54; lateral margins curved; apex less narrowed than in *C. mexicanum*, anterior angles more distinct; base moderately narrowed; basal impressions larger than in *C. mexicanum*, about 0.3 of length of pronotum; basal impression closed posteriorly, open laterally; outer marginal groove completely hidden in dorsal view, as deep as inner marginal groove; prosternum without precoxal setae.

All striae impressed, pollinose, including supramarginal, marginal; sutural stria with two or three setae near apex; intercalary stria without setae; intratubercular stria with complete row of five or six setae; marginal stria with five or six setae near apex; transverse sulci of abdomen broadly interrupted in midline, without pits at medial ends; Sternum VI of abdomen shallowly impressed near apex in both sexes, in profile forming distinct angle; Sternum VI coarsely punctate, most punctures elongate, some reaching margin of sternum (Fig. 102); lateral pit of Sternum IV of female, large glabrous; anterior femur of male with large, broad, rather obtuse ventral tooth; surface proximal to tooth tuberculate; tooth without setae; anterior trochanter of male dentate; anterior tibia of male with large proximal tooth (Fig. 84); middle calcar acute, scarcely raised above level of spurs; hind calcar small, acute, elevated well above spurs; proximal margin of hind calcar slightly emarginate.

This species is unique in having elongate, slightly confluent punctures on abdominal Sternum VI. The pronotum is not as narrowed anteriorly as in *C. mexicanum*. The shape of the pronotum, the well developed outer marginal groove which is hidden in dorsal view, and the numerous elytral setae, all suggest *C. blomi*. The latter species, however, has four large impressions on Sternum VI, rather than elongate punctures.

The species is named for the collector, Michael A. Ivie, to whom we are grateful for the opportunity to study the type series.

SUBGENUS *PROTAINOA* BELL AND BELL 1978

Type species.— *Clinidium (Protainoa) extrarium* Bell and Bell 1978.

Description.— Antennal stylet slender, acuminate, long; tufts of minor setae present on Segments VI-X; one or two temporal setae present; orbital groove abbreviated posteriorly; marginal groove of pronotum single; angular seta,

marginal setae absent; sternopleural groove absent; elytral striation reduced; marginal stria fifth complete stria from suture; supramarginal stria represented by sparse row of fine punctures below intratubercular stria; sutural, parasutural, intercalary, intratubercular striae complete; setae present in sutural, intercalary, intratubercular, marginal striae; metasternum with broad median concavity, which is continued posteriorly to abdominal Sternum III; female with lateral pit on abdominal Sternum IV; male with anterior trochanter dentate; all femora of male with ventral surface tuberculate; tubercles most numerous on anterior femur; anterior femur of male with inconspicuous ventral tooth; male without proximal tooth on anterior tibia; base of anterior tarsus distad to cleaning organ; calcaria small; middle one longer but more slender, more acute than hind one; latter triangular, its apex acute, slightly proximad of level of spurs; hind tibia of male with medial apical tooth, resembling third spur.

Clinidium (Protainoa) extrarium Bell and Bell 1978

(Fig. 87)

Clinidium (Protainoa) extrarium Bell and Bell 1978: 63-64.

Type Material.— HOLOTYPE male, labelled: "Am. Bor. Rhysodes", "N. Amerika" (BSL) PARATYPE female, same data (BSL).

Description.— Length 6.1-6.3 mm. Antenna with basal setae present on Segments VII-X; head slightly longer than wide; median lobe short, tip acute, opposite anterior margin of eye; medial margins of temporal lobes slightly curved; posterior margin of temporal lobe long, pilose; temporal lobe with two prominent, isolated punctures, probably both setose (but setae probably broken off in type series); holotype with only one puncture on right side.

Pronotum elongate; length/greatest width 1.67; widest at basal 0.33; strongly tapered anteriorly; basal impressions deep, oval, closed posteriorly; length of basal impression 0.16 of length of pronotum; hind angle with prominent tooth, preceded by pollinose pit.

Sutural, parasutural, intercalary stria impressed, coarsely punctate, entire; intratubercular stria impressed near apex, remainder not impressed, represented by row of fine punctures; marginal stria impressed, coarsely punctate near apex, effaced in middle 0.33, represented by row of fine punctures near humerus; sutural stria with two setae near apex; intercalary stria with complete row of four setae; intratubercular stria with two setae near apex; marginal stria with several setae near apex; metasternum with large transverse curved pilose area near anterior margin; transverse sulci of Sterna III-V prominent, rather narrowly interrupted at midline, medial, lateral ends each with prominent pits; in male, Sterna III-V also each with median pit; female with median pit on Sternum III but not on other sterna; Sternum VI with transverse sulci near base, curved submarginal sulci near apex; latter very narrowly interrupted at midline.

This isolated species resembles its nearest relatives in subgenus *Tainoa* in the shape of the pronotum, but differs strongly in having much more complete elytral striation, denticulate hind angles, and in lacking all pronotal setae.

The country of origin is unknown. We think it likely to be the tropical lowlands of Mexico or northern Central America. It seems likely that the endemic subgenus *Tainoa* of the Greater Antilles is derived from an ancestor much like *C. extrarium*.

SUBGENUS *TAINOA* BELL AND BELL 1978

Type species.— *Clinidium darlingtoni* Bell 1970.

Description.— Antennal stylet acuminate, long; tufts of minor setae present on antennal Segments VI-X; basal setae present on Segments VI-X; two or three temporal setae; orbital groove present, abbreviated at posterior margin of eye; marginal groove of pronotum single; angular, one or more marginal setae present; sternopleural groove absent; elytral striation strongly reduced; parasutural stria effaced anteriorly, reduced to remnant in posterior part of elytron; supramarginal not impressed, represented by row of punctures, incomplete; metasternum neither sulcate not impressed; female with lateral pit in Sternum IV; Sternum VI with two pairs of impressions, both oblique, posterior pair divergent posteriorly; in some specimens with additional pair of round anteriomedial pits; anterior femur with cleaning organ very large, entirely proximad to base of anterior tarsus; anterior trochanter of male dentate; anterior femur of male without ventral tooth.

Phylogeny.— The two Cuban species, *C. curvicosta* and *C. chevrolati* are obviously closely related, differing mainly in secondary sexual characters. *C. xenopodium*, of Hispaniola, and *C. darlingtoni*, of Jamaica, are rather distantly related to one another, but share enough characters, including a strongly abbreviated parasutural stria, to suggest that they are descended from a common ancestor different from that which led to the Cuban species.

KEY TO SPECIES

- 1 Parasutural stria relatively long, anterior and near middle of elytron 2
- 1' Parasutural stria very short, arising at or behind apical 0.33 of elytron 5
- 2 (1) Males, calcars present 3
- 2' Females, calcars absent 4
- 3 (2) Hind calcar with dorsal margin slightly sinuate, largest seta of hind calcar smaller, scarcely longer than width of calcar
..... *C. curvicosta* Chevrolat, p. 71
- 3' Hind calcar with dorsal margin strongly angulate, largest seta more than twice as long as width of calcar *C. chevrolati* Reitter, p. 74
- 4 (2') Sternum VI sloped gradually posteriorly, in profile view angulate
..... *C. curvicosta* Chevrolat, p. 71
- 4' Sternum VI strongly impressed posteriorly, anterior margin of impression forming median tubercle; in lateral view, tubercle forming sharp angle ...
..... *C. chevrolati* Reitter, p. 74
- 5 (1') Parasutural stria not attached to intercalary anteriorly; intercalary ending blindly posteriorly *C. darlingtoni* Bell, p. 74
- 5' Parasutural stria attached to intercalary stria both anteriorly and posteriorly, isolating small remnant of Interval III
..... *C. xenopodium* Bell, p. 75

Clinidium (Tainoa) curvicosta Chevrolat 1873a

(Figs. 88, 93, 94)

Clinidium curvicosta Chevrolat 1873a: 215.*Clinidium (Tainoa) curvicosta* (Chevrolat) Bell and Bell 1978.

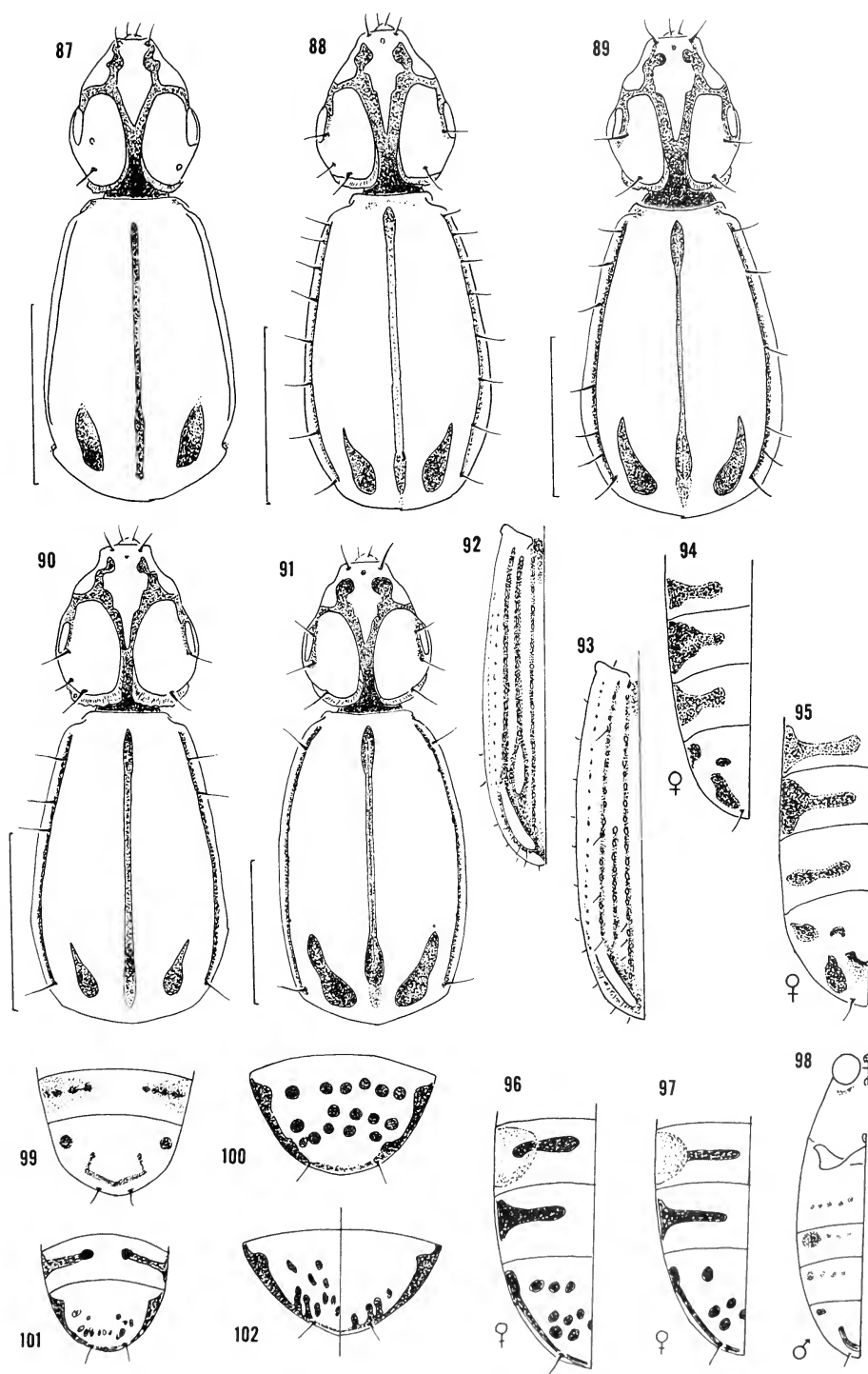
Type Material.— Not seen by us. According to the original description, collected in Cuba by F. Poey. Vulcano and Pereira (1975b) illustrated the elytron of a specimen in the Museum of Natural History in Vienna, which is labelled as the type. As previously noted (Part 1:64), this specimen does not correspond to the original description, and probably is labelled incorrectly. The original description could apply either to the present species, or to the one subsequently described as *C. chevrolati*. Until an authentic type is located, it seems best to continue to use the Chevrolat name for the present species, as was the practice of Bell (1970) and previous authors.

Description.— Length 4.3–6.2 mm (according to Chevrolat, the type measured 8 mm). Basal setae present on antennal Segments VII–X; median lobe of head elongate, tip acute, opposite posterior margin of eye; medial margins of temporal lobe nearly parallel opposite frontal space; medioposterior margin of temporal lobe nearly evenly rounded, completely fringed with pilosity; temporal lobe with 3 setae in most specimens, two opposite eye, one near occiput; either anterior or posterior of those near eye absent in some specimens.

Pronotum elongate, length/greatest width 1.74; basal impression about 0.15 of total length of pronotum; in most specimens, basal impression pointed, suggesting rudimentary distal striae, four or five marginal setae.

Sutural stria impressed, entire, punctate; parasutural impressed, punctate, base near middle of elytron, not connected to neighboring striae, apex connected to intercalary stria; intercalary stria entire, impressed, punctate; intratubercular impressed near apex, otherwise not impressed, represented by row of coarse punctures; supramarginal effaced at base, apex, middle 0.33 represented by row of punctures; marginal stria coarsely punctate, shallowly impressed; sutural stria with four to six setae in nearly complete row, though absent from basal 0.25; intercalary stria with complete row of seven or eight setae; intratubercular stria with three to five setae in apical 0.25; marginal stria with 10–12 setae forming nearly complete row, though absent from basal 0.25 (Fig. 93); Sternum VI with reflected margin, anteriomedial pits present in most specimens, absent in 1; anteriolateral pits elongate; posterior pits convergent posteriorly, connected by fine submarginal groove (Fig. 94); anterior tibia of male with proximal tooth small, opposite proximal end of cleaning organ; calcars very small; hind calcar triangular, dorsal margin nearly straight, largest seta scarcely longer than width of calcar; lateral pit of Sternum IV of female laterad to sulcus; Sternum VI in female similar to that of male, only slightly concave in lateral view; neither impressed nor tuberculate, female with tip of elytra evenly rounded in posterior view.

Plate 8. Fig. 87. Genus *Clinidium*, Subgenus *Protainoa*, Head and pronotum, dorsal aspect, *C. (P.) extrarium* Bell and Bell. Figs. 88–95. Genus *Clinidium*, Subgenus *Tainoa*; Figs. 88–91, Head and pronotum, dorsal aspect; Fig. 88, *C. (T.) curvicosta* Chevrolat; Fig. 89, *C. (T.) chevrolati* Reitter; Fig. 90, *C. (T.) darlingtoni* Bell; Fig. 91, *C. (T.) xenopodium* Bell; Figs. 92–93, Left elytron, dorsal aspect; Fig. 92, *C. (T.) xenopodium* Bell; Fig. 93, *C. (T.) curvicosta* Chevrolat; Figs. 94–95, Sterna III–VI, right half, female; Fig. 94, *C. (T.) curvicosta* Chevrolat; Fig. 95, *C. (T.) chevrolati* Reitter. Figs. 96–102. Genus *Clinidium*, Subgenus *Mexiclinidium*. Fig. 96–97, Sterna IV–VI, right half; Fig. 96, *C. (M.) triplehorni* new species, female; Fig. 97, *C. (M.) balli* new species, female; Fig. 98, Metasternum, abdomen, right half, male *C. (M.) championi* new species; Figs. 99, 101, Sterna V–VI; Fig. 99, *C. (M.) halffteri* new species; Fig. 101, *C. (M.) guatemalenum* Sharp; Figs. 100, 102, Sternum VI; Fig. 100, *C. (M.) mexicanum* Chevrolat; Fig. 102, *C. (M.) iviei* new species (bisected, showing range of variation).



The relatively long parasutural stria, 0.5 the length of the elytron, distinguishes this species from all others except *C. chevrolati*. From the latter, the male can be distinguished by the triangular hind calcar with a relatively short major seta, and the female by the unmodified Sternum VI.

Range.— Cuba, central and eastern part of the Sierra Maestra. Bell (1970) lists localities.

Clinidium (Tainoa) chevrolati Reitter 1880
(Figs. 89, 95)

Clinidium chevrolati Reitter 1880: 30-31.

Clinidium turquinense Bell 1970.

Clinidium (Tainoa) chevrolati (Reitter) Bell and Bell 1978.

Type Material.— For *C. chevrolati* HOLOTYPE female, labelled: "Neu Granada, Chevr., type Cl., *granatense*, *chevrolati* Reitter" (NMW). It is not clear why this specimen should be labelled as a type of *C. granatense*. It does not match the description of the latter species, which is represented by another type, belonging to Subgenus *Clinidium* s. str. (NMW). The type specimen of *C. chevrolati* undoubtedly bears an incorrect locality label, as it appears identical to *C. turquinense* of Cuba. For *C. turquinense* HOLOTYPE male, labelled: "Pico Turquino, 3000-5000 ft., June, 1936, coll. P. J. Darlington" (MCZ 31752). PARATYPE one female, with head, prothorax missing, same data as type (MCZ).

Description.— Length 6.8-7.0 mm. Very similar to *C. curvica* except for the following points: body more robust; pronotum less elongate, length/greatest width 1.60; five or six marginal setae; sutural stria with only two to four setae limited to portion behind middle; hind calcar of male very large, strongly angulate on proximal margin, with very long, curved seta; female with Sternum VI deeply impressed in posterior 0.5, impression preceded by median tubercle (Fig. 95); female with tips of elytra separately angulate in posterior view.

Range.— Pico Turquino is the western Sierra Maestra of Cuba, and outside the known range of *C. curvica*.

Clinidium (Tainoa) darlingtoni Bell 1970
(Fig. 90)

Clinidium (s. str.) *darlingtoni* Bell 1970: 317-318.

Clinidium (Tainoa) darlingtoni (Bell) Bell and Bell 1978.

Type Material.— HOLOTYPE male, labelled: "Whitfield Hall, St. Thomas parish, JAMAICA, Jan. 9, 1967, coll. R. T. Bell, J. R. Bell, B. B. Chiolino" (MCZ 31751). PARATYPES ten males, five females, same data as holotype (MCZ, UVM); two males, same locality, coll. P. J. Darlington, Aug. 13-20, 1934 (MCZ).

Description.— Length 4.9-6.7 mm. Basal setae present on antennal Segments VIII-X; median lobe elongate, tip acute, opposite posterior margin of eye; medial margins of temporal lobes parallel, rather close together; medioposterior margin of temporal lobe nearly evenly rounded, fringed with pilosity; temporal lobe with three setae (preorbital, postorbital, occipital).

Pronotum relatively short; length/greatest width 1.58; basal impression very small, about 0.10 of length of pronotum; three or four marginal setae, one near angular seta, others anterior to middle of pronotum.

Sutural stria shallowly impressed, very coarsely punctate; parasutural stria deeply impressed, coarsely punctate, base far posterior to middle of elytron, not connected to neighbouring striae; apex attached to intratubercular stria; intercalary stria very deeply impressed, coarsely punctured, ending posteriorly just anterior to base of parasutural stria; interval laterad to intercalary stria elevated, forming medial-facing scarp; intratubercular stria impressed near apex, otherwise represented only by row of very minute punctures; supramarginal stria absent; marginal stria with basal 0.33 entirely effaced, middle 0.33 represented by row of minute punctures; apical 0.33 impressed; sutural stria with three or four setae near apex; intercalary stria with six to eight setae forming complete row; intratubercular stria with three or four setae near apex; marginal stria with seven or eight setae in apical 0.25.

Sternum VI with reflected margin; anteriomedial pits absent; anteriolateral pits elongate; posterior pits convergent posteriorly; anterior tibia of male with proximal tooth small, opposite proximal end of cleaning organ; calcars small, hind one scarcely larger than middle one; hind calcar angulate to proximal margin, with small, proximally directed seta; lateral pit of Sternum IV of female large, triangular, with short trace of transverse sulcus medial to it; Sternum VI of female slightly concave in lateral view, but not distinctly impressed.

This species is easily recognized by the very short parasutural stria which ends blindly anteriorly, close to the blind posterior end of the intercalary stria.

Range.—Jamaica from sea level to 4500'. Not known from west of Runaway Bay and Mt. Diable. Bell (1970) gives a list of localities. In addition, we have studied a series of eight specimens labelled: "JAMAICA, St. Andrew Parish, Hardwar Gap, 4000', J. Peck, 16, XII, 1972" (BSRI).

Clinidium (Tainoa) xenopodium Bell 1970

(Figs. 91, 92)

Clinidium (sensu stricto) xenopodium Bell 1970: 316.

Clinidium (Tainoa) xenopodium (Bell) Bell and Bell 1978.

Type Material.—HOLOTYPE male, labelled: "Loma Vieja, near Santa Constanza, Dominican Republic, 6000 ft., August 1938, coll. P. J. Darlington" (MCZ 31750). PARATYPES two males, one female, labelled: "La Cavite, Dominican Republic, March 5, 1917, coll. R. H. Beck" (MCZ, UVM).

Description.—Length 5.8–6.5 mm. Basal setae present on antennal Segments VII–X; median lobe short, tip acute, opposite middle of eye; medial margins of temporal lobes divergent posteriorly; occipital angle glabrous, prominent, interrupting fringe of pollinosity on margin of temporal lobe; temporal lobe with three setae, preorbital, postorbital, occipital.

Pronotum moderately elongate, length/greatest width 1.65; basal impression oval, about 0.25 of length of pronotum; one marginal seta near apex of pronotum, also one angular seta.

Sutural stria impressed, finely punctate; parasutural stria impressed, short, joined at both ends to intercalary stria, isolating small oval area; intercalary stria entire, impressed, finely punctate; intratubercular stria impressed near apex, otherwise represented by row of minute punctures; supramarginal stria effaced at base, apex, represented by row of fine punctures in middle 0.33 of elytron; marginal stria deeply impressed at apex, remainder shallow impressed; sutural stria with two or three setae near apex, or else these setae on Interval I, medial to sutural stria; intercalary stria with four setae near apex; intratubercular stria with two setae near apex; marginal stria with seven or eight setae in posterior 0.5 (Fig. 92).

Sternum VI of abdomen without raised rim; anteriomedial pits absent; anteriolateral pits elongate; posterior pits parallel or divergent posteriorly; anterior tibia of male with proximal tooth large, distinctly proximad to cleaning organ; calcar very large; middle calcar narrowly triangular, acute, 0.33 as long as tibia; hind calcar broadly triangular, apex acuminate, calcar more than 0.5 as long as tibia; female with lateral pit of Sternum IV very large, rounded medially, without trace of transverse sulcus medial to it; Sternum VI of female not impressed posteriorly.

The short parasutural stria, connected both anteriorly and posteriorly to the intercalary stria, is diagnostic of this species.

SUBGENUS *ARCTOCLINIDIUM* BELL 1970

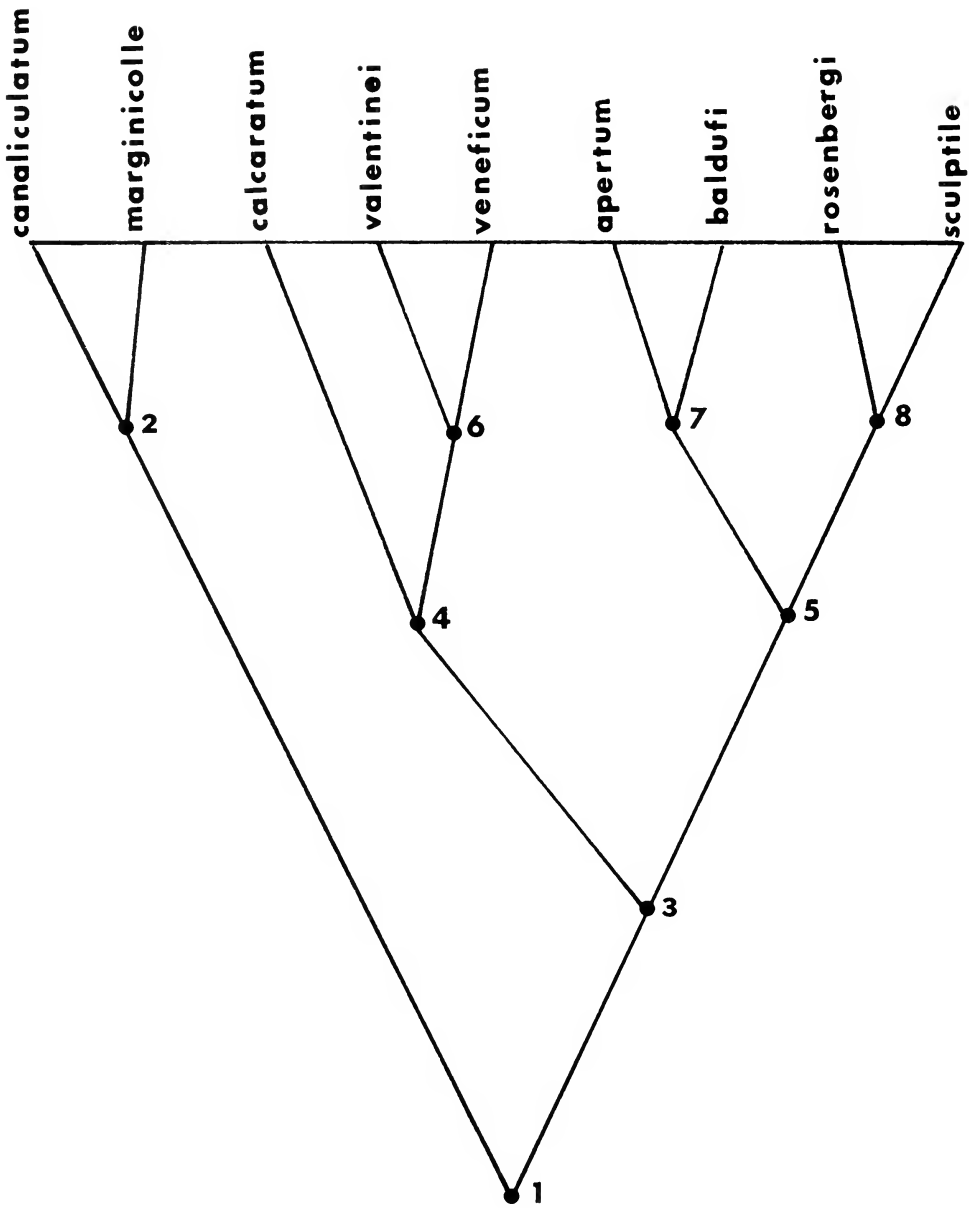
Type species.—*Clinidium sculptile* (Newman)

Description.—Antennal stylet small; tufts of minor setae present on Antennal Segments VI–X (*C. veneficum*) or VII–X (all other species); temporal seta one or absent; eye crescentic; orbital groove complete, joined posteriorly to marginal pollinosity of temporal lobe; pronotum with lateral margins curved, base, apex truncate; marginal groove double or single; pronotum with angular seta present (*C. marginicollae*) or absent (all other species); marginal setae absent; sternopleural groove present or absent; elytral striation complete; marginal stria sixth from suture; inner intervals of elytron convex or costate; elytral setae very few, at most one in apex of parasutural or sutural stria, several in apex of marginal stria, one on apical tubercle; metasternum with or without median sulcus; female with enlarged lateral pit on Sternum III or IV or both; base of anterior tarsus opposite cleaning organ.

The more distal position of the cleaning organ and the relatively few elytral setae separate this subgenus from *Mexiclinidium*. North American species have the inner intervals costate, and look similar to the larger *Mexiclinidium*, from which they can be distinguished by the presence of the sternopleural groove and the complete intercalary stria. European and western Asian species have the intervals not costate, and lack the sternopleural grooves.

This subgenus is Holarctic. It has five species in the eastern U.S.A., and one each on the Pacific Coast of North America, Japan, the Caucasus, and Southern Europe.

Phylogeny.—Our concept of the interrelationship of the nine species are as illustrated in Diagram 2. The subgenus is derived from two ancestral populations, Species 2 and Species 3,



Phylogenetic Diagram 2. Reconstructed Phylogeny of species of *Clinidum* Subgenus *Arctoclinidium*

both descended from the common ancestor, Species 1. From Species 2 have arisen the two European species, *C. canaliculatum* and *C. marginicolle*. They are characterized by the following features: elytral intervals not carinate, though convex; sternopleural groove absent; precoxal setae present; parasutural stria incomplete at apex, so Intervals II, III fuse posteriorly; supramarginal row of punctures, not impressed; marginal stria not impressed except at extreme apex; one seta near apex of either sutural or parasutural stria; abdominal sterna in both sexes glabrous medially.

Species 3 was the ancestor of the six North American and one Japanese species. Among these species, the inner elytral intervals are carinate, the sternopleural groove is present; precoxal setae are absent; parasutural stria is complete, so Intervals II, III do not fuse; the supramarginal stria is impressed; marginal is completely impressed; setae are absent from apices of inner elytral striae, and the abdominal sterna of the male have a pattern of pollinose areas.

Synapomorphies of Species 2 and its descendants include loss of sternopleural groove; loss of apex of parasutural stria; possible synapomorphies are the reduction of marginal and supramarginal striae. Synapomorphies of Species 3 and its descendants are the development of ventral pollinosity in the male, the highly costate elytral intervals, and possibly the loss of setae from the apex of the sutural or parasutural striae.

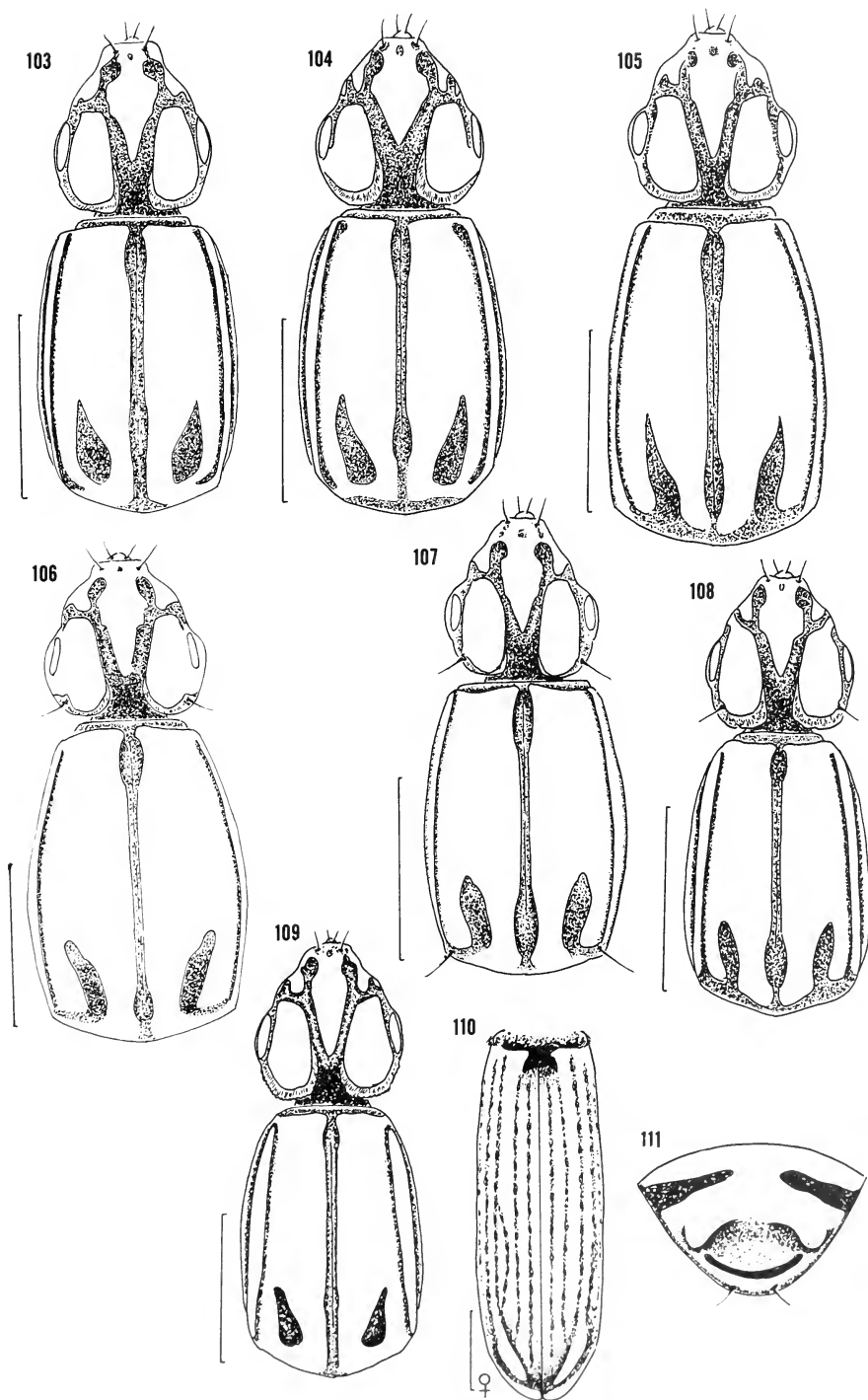
The interpretation of the costate intervals is debatable. Noncostate, slightly convex intervals are found in most Rhysodini with functional hind wings, and probably represent the primitive character state for the tribe. Costate intervals have arisen several times, and can be regarded as advanced. However, it is quite possible that the costae can be reduced secondarily. Within *Clinidium*, both *Mexiclinidium* and *Arctoclinidium* have costate and noncostate species, and in the more highly modified members of subgenera *Tainoa* and *Clinidium sensu stricto*, the intervals are not costate. Thus, Species 2 may have lost its costae secondarily. The absence of the specialized pollinose areas on the abdomen of the male, however, suggests that Species 2 and its descendants are a separate phyletic line from the costate species.

Species 2 probably had the intercalary stria unmodified. The status of other characters is less definite. *C. marginicolle* is the only member of the subgenus to have an angular seta. It could be argued that this seta has been lost separately in *C. canaliculatum*, and in Species 3. However, in Rhysodini generally the greatest number of tactile setae are found in highly modified species with cryptic habits and strongly reduced eyes. This might imply that a proliferation of tactile setae has happened independently, and that the angular seta has appeared *de novo* in *C. marginicolle*. There are similar possibilities in relation to the presence of a temporal seta in both species descended from Species 2, and in *C. valentinei* alone among those descended from Species 3. Either *C. valentinei* retains the temporal seta, which was lost independently in *C. veneficum*, *C. calcaratum* and Species 5, or else the temporal seta was developed independently in *C. valentinei* and in Species 2.

Species 3 probably gave rise to Species 4 and 5. In Species 5, the metasternum developed a longitudinal sulcus. The four species descended from it are much alike, and all are found in eastern North America. The existence of Species 4 is less strongly indicated than that of Species 5. There are no clearly derived characters in common among *C. veneficum*, *C. valentinei*, and *C. calcaratum*, though a possible synapomorphy is the fact that the pollinose area of Sternum II is narrowed anteriorly, while in the remaining species, it is as wide or wider anteriorly than posteriorly. Otherwise, the three species without a sulcus are more widely divergent from one another than are those with a sulcus, and are widely distributed, with one

	with ventral tooth	<i>C. marginicollae</i> Reitter, p. 83	
3 (1')	Metasternum without median sulcus		4
3	Metasternum with median sulcus		9
4 (3)	Males, calcars present		5
4'	Females, calcars absent		7
5 (4)	Anterior femur without ventral tooth; hind trochanter pointed		
		<i>C. calcaratum</i> Leconte, p. 84	
5'	Anterior femur with ventral tooth; hind trochanter rounded		6
6 (5')	Posterior femur with ventral tooth; anterior trochanter pointed		
		<i>C. valentinei</i> Bell, p. 85	
6'	Posterior femur without ventral tooth; anterior trochanter rounded		
		<i>C. veneficum</i> Lewis, p. 88	
7 (4')	Lateral pit of abdominal Sternum III enlarged		
		<i>C. valentinei</i> Bell, p. 85	
7'	Lateral pit of Sternum IV enlarged		8
8 (7')	Marginal carina of pronotum linear; outer marginal groove not visible in dorsal view; basal impression of pronotum open posteriorly		
		<i>C. calcaratum</i> Leconte, p. 84	
8'	Marginal carina relatively broad; outer marginal groove visible in dorsal view; basal impression closed posteriorly		
		<i>C. veneficum</i> Lewis, p. 88	
9 (3')	Males, calcars present		10
9'	Females, calcars absent		13
10	Prosternum glabrous		11
10'	Prosternum with median pollinose area		12
11 (10)	Abdominal Sternum V with pollinosity interrupted by narrow median carina; anterior tibia without proximal tooth		
		<i>C. baldufi</i> Bell, p. 89	
11'	Abdominal Sternum V without median carina; anterior tibia with proximal tooth		
		<i>C. apertum</i> Reitter, p. 90	
12 (10')	Pollinose area present between transverse sulci on Sternum V; hind calcar large		
		<i>C. sculptile</i> (Newman), p. 92	
12'	Sternum V glabrous between transverse sulci; hind calcar very small		
		<i>C. rosenbergi</i> Bell, p. 91	
13 (9')	Lateral pit in Sternum III of abdomen		14
13'	Lateral pits present in Sterna III, IV		15
14 (13)	Sternum VI with posterior 0.5 deeply impressed; cauda of elytra prominent, trapezoidal		
		<i>C. baldufi</i> Bell, p. 89	
14'	Sternum VI with posterior 0.5 not impressed; cauda small, rounded		
		<i>C. apertum</i> Reitter, p. 90	
15 (13')	Lateral pits of Sterna III, IV equally large; cauda very small, rounded; Sternum VI impressed in some specimens, not impressed in others		
		<i>C. rosenbergi</i> Bell, p. 91	
15'	Lateral pits of Sternum IV smaller than those of Sternum III; cauda prominent, rounded; Sternum VI with posterior 0.5 deeply impressed		
		<i>C. sculptile</i> (Newman), p. 92	

Plate 9. Figs. 103–111. Genus *Clinidium*, Subgenus *Arctoclinidium*. Figs. 103–109, Head and pronotum, dorsal aspect; Fig. 103, *C. (A.) rosenbergi* Bell; Fig. 104, *C. (A.) baldufi* Bell; Fig. 105, *C. (A.) calcaratum* Leconte; Fig. 106, *C. (A.) canaliculatum* (Costa); Fig. 107, *C. (A.) marginicollae* Reitter; Fig. 108, *C. (A.) valentinei* Bell; Fig. 109, *C. (A.) veneficum* Lewis; Fig. 110, Elytra, dorsal aspect (showing stria variation), *C. (A.) veneficum* Lewis; Fig. 111, Sternum VI, *C. (A.) veneficum* Lewis.



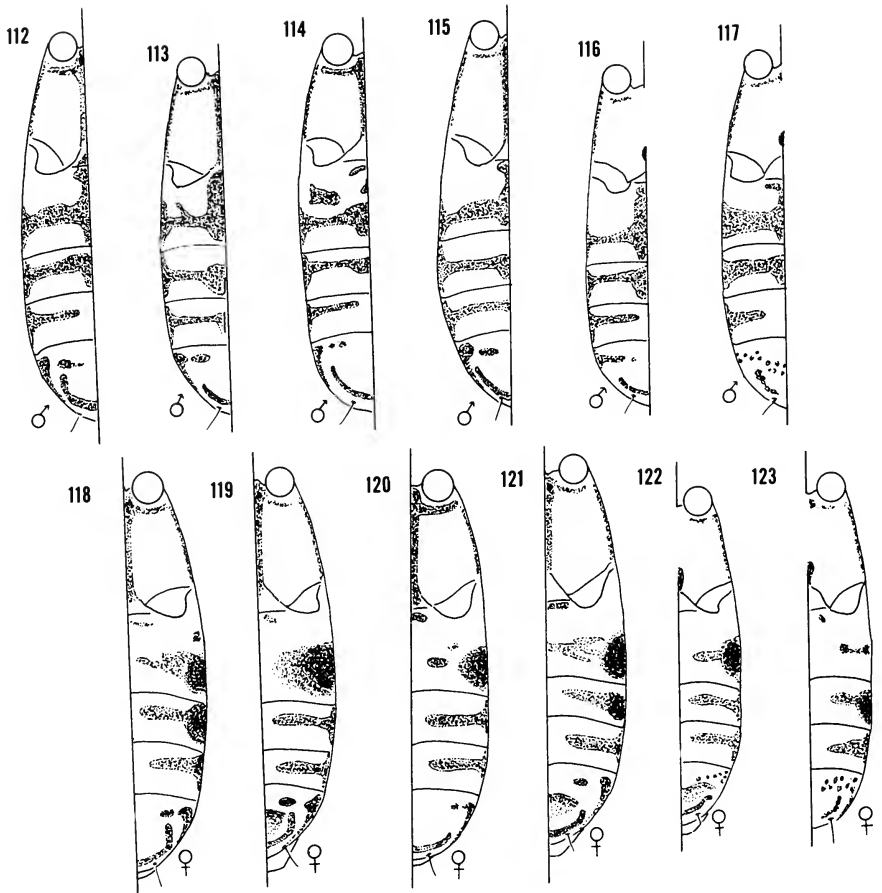


Plate 10. Figs. 112–123. Genus *Clinidium*, Subgenus *Arctoclinidium* *Metasternum*, abdomen, halved. Figs. 112, 118, *C. (A.) rosenbergi* Bell; Figs. 113, 119, *C. (A.) baldufi* Bell; Figs. 114, 120, *C. (A.) apertum apertum* Reitter; Figs. 115, 121, *C. (A.) sculptile* (Newman); Figs. 116, 122, *C. (A.) valentinei* Bell; Figs. 117, 123, *C. (A.) calcaratum* Leconte.

Clinidium (Arctoclinidium) canaliculatum (Costa 1839)
(Fig. 106)

Ips canaliculatus Costa 1839: 104.

Rhyzodes trisulcatus Germar 1840: 441.

Rhyzodes sulcipennis Mulsant 1853: 6.

Clinidium trisulcatum (Germar) Chevrolat 1873a.

Clinidium canaliculatum (Costa) Grouvelle 1903.

Clinidium (Arctoclinidium) canaliculatum (Costa) Bell and Bell 1978.

Type Material.— We have not located type material for any of the three nominate species of *Clinidium* described from southern Europe. As there appears to be only one species of *Clinidium* in Europe, we follow Grouvelle (1903) in regarding *R. trisulcatus* Germar and *R. sulcipennis* Mulsant as being pure synonyms.

Description.— Length 6.0-7.5 mm. Antennal Segments VII-X with tufts of minor setae; basal setae sparse, limited to Segments IX-X; one temporal seta present; pronotum rather short, length/greatest width about 1.47; greatest width of pronotum slightly behind middle; pronotum strongly narrowed anteriorly, only slightly narrowed posteriorly; angular seta absent; basal impressions open posteriorly; outer marginal groove not visible in dorsal view, in most specimens abbreviated anteriorly; precoxal setae present on prosternum; sternopleural groove absent.

Elytral striae punctate; sutural stria complete, shallowly impressed; parasutural impressed, abbreviated near apex; intercalary stria much deeper than other striae; portion between 0.55 and 0.70 of length deeper but scarcely wider than remainder; intratubercular stria shallowly impressed; supramarginal stria not impressed, represented by line of very fine punctures near middle of elytron; base, apex effaced; marginal stria effaced at base, middle portion not impressed, represented by line of rather coarse punctures; apex impressed; Intervals I-III broad, nearly flat, of nearly uniform width; Interval IV not flattened laterad to deepened part of intercalary stria; elytron with one seta in apex of sutural stria, absent or one in apex of intercalary stria; two to four near apex of marginal stria.

Metasternum not sulcate; transverse sulci of abdominal sterna widely separated in midline, without median pollinosity in either sex; Sternum VI coarsely punctate; female with lateral pits on abdominal Sternum IV; Sternum VI of female without impression; male with anterior, posterior trochanters pointed; male without ventral tooth on anterior femur, without proximal tooth on anterior tibia; middle calcar acute, narrow; hind calcar large, somewhat cultrate, dorsal margin curved, ventral margin shallowly emarginate; male with prosternum, abdominal sterna glabrous.

This species is similar to *C. marginicolle*, from which it differs in the absence of the angular seta, in the wider, flatter elytral intervals, and in the smaller, narrower subapical enlargement of the intercalary stria. The males can also be distinguished by the different shape of the hind calcar, and by the absence of the ventral tooth on the anterior femur in *C. canaliculatum*. Some specimens of *C. canaliculatum* resemble *C. marginicolle* in having a complete outer marginal groove on the pronotum, although it is not visible except in lateral view.

Range.— Southern Italy (Sicily, Calabria), Greece. We have studied specimens with specific locality labels: GREECE: Taygetos, Morea (CNHM, UVM). ITALY: Aspromonte, Calabria (CNHM); Sta. Eufemia, Calabria (CNHM, UVM). Hincks (1950) and earlier authors also record it from the Caucasus. We have not seen this species from the Caucasus, and believe that records from there are misidentified *C. marginicolle*.

Clinidium (Arctoclinidium) marginicolle Reitter 1889
(Fig. 107)

Clinidium marginicolle Reitter 1889: 23.

Clinidium (Arctoclinidium) marginicolle (Reitter) Bell and Bell 1978.

Type Material.— We have not located authentic type material. According to the original description, the type series was from Lenkoran (Azerbaijan), and was collected by Leder. A specimen in the Natural History Museum of Vienna is labelled as a type, but is labelled: "PERSIA: Kopet Dag, Siaret 1160 m., 5.99, Col. Hauser". The label probably indicates that Reitter compared it with his type series and considered it identical.

Description.— Length 5.8-7.5 mm. Antennal Segments VII-X with tufts of minor setae; basal setae few, limited to Segment X; one temporal seta; pronotum more elongate than in *C. canaliculatum*, length/greatest width about 1.57; widest near middle; base more narrowed than in *C. canaliculatum*, nearly as narrow as apex; angular setae present; basal impressions closed posteriorly or almost closed; outer marginal groove deep, complete, barely visible in dorsal view; prosternum with precoxal setae; sternopleural groove absent.

Elytral striae punctate; sutural stria complete, shallowly impressed; parasutural impressed, abbreviated near apex, sinuate opposite dilated portion of intercalary stria; latter very deeply impressed; portion between 0.55, 0.70 of length deeper, wider than remainder; intratubercular stria shallowly impressed; supramarginal stria almost absent, represented by a few minute punctures near middle; marginal stria effaced at apex, marginal stria effaced at base, middle portion not impressed, represented by row of punctures; apex impressed; sutural interval of even width, nearly flat; Interval II similar

to sutural interval in anterior 0.5, posteriorly much narrower than sutural interval, convex, slightly sinuate opposite depressed part of intercalary stria; Interval III slightly convex, as broad as sutural interval, depressed opposite depressed part of intercalary stria; Interval IV broad, slightly convex except opposite depressed part of intercalary stria, where narrowed, depressed; elytron without setae or one in apex of sutural stria, one seta in intercalary stria opposite apex of parapsutural stria, one near apex of intratubercular stria, two to four apex of marginal stria.

Metasternum not sulcate, transverse sulci of abdominal sterna rather narrowly separated in midline, without median pollinosity in either sex; Sternum VI coarsely punctate; female with lateral pits on abdominal Sternum IV; Sternum VI of female without impression; male with anterior, posterior trochanters pointed; male with small, obtuse ventral tooth on anterior femur; male without proximal tooth on anterior tibia; middle calcar small, acute, triangular; hind calcar small, with dorsal margin angulate, ventral margin straight, well above spurs; male with prosternum, abdominal sterna glabrous.

This species differs from *C. canaliculatum* in having an angular seta, in having a longer, narrower pronotum, and in the shape of the calcars. Also, the subapical enlargement of the intercalary stria is more conspicuous, and alters the neighbouring intervals and striae.

Range.—Caucasus Mountains of the southern U.S.S.R. and the Kopet Dag range of northeastern Iran. We have studied specimens from the following localities: IRAN, Siaret, Kopet Dag (NMW; NMHB, CNHM); Astrabad (MNHB); U.S.S.R. Paleton, 1200', Astar. R., Talysh. (LEN).

Clinidium (Arctoclinidium) calcaratum LeConte 1875

(Figs. 105, 117, 123)

Clinidium calcaratum LeConte 1875: 164.

Clinidium (Arctoclinidium) calcaratum (LeConte) Bell 1970.

Type Material.—HOLOTYPE sex not recorded, labelled: "Vanc." (MCZ 6831). In the original description the type locality is cited as "Vancouver Island".

Description.—Length 5.8-8.1 mm. Antennal Segments VII-X with tufts of minor setae; basal setae sparse, limited to Segments IX, X; temporal seta absent; pronotum relatively elongate, length/greatest width about 1.59; widest posteriorly, base slightly narrowed, apex strongly so; sides of pronotum only slightly curved; angular seta absent; basal impressions relatively large, open posteriorly; outer marginal groove scarcely visible in dorsal view, close to inner marginal groove, separated by narrow nearly linear marginal carina; precoxal setae absent; sternopleural groove present.

Elytral striae deep, broad, inconspicuously punctate; supramarginal stria shallower than the others; intervals narrow, costate; intercalary not abbreviated posteriorly in most specimens, in a few specimens very shortly abbreviated on one elytron; Intervals II, III not united posteriorly except as a unilateral aberration; elytron entirely without setae; cauda small, rounded, present in both sexes.

Prosternum glabrous in both sexes; metasternum not sulcate; transverse sulci widely separated at middle; male with pollinosity of Sternum II a narrow rectangle; male with median pollinose areas present on Sterna I-IV, absent from Sternum V; Sternum VI varying geographically (see below, under *variation*); female with lateral pits on Sternum IV; anterior, posterior trochanters of male pointed; male without ventral tooth on anterior, posterior femora, without proximal tooth on anterior tibia; hind calcar very large, 0.5 as long as hind tibia.

This is the only member of the genus in western North America. The male is easily recognized by the very large hind calcar, while the female differs from all species with carinate intervals other than *C. veneficum* in having the lateral pits in abdominal Sternum IV but not Sternum III. The narrow marginal carina and the absence of a tuft of minor setae on antennal Segment VI will separate it from the latter species.

Range.—Substantially as listed by Bell (1970), in the Coast Range and Sierra Nevada of California, from Mendocino and Tuolumne Counties northwards. In Oregon, known from a number of localities in Klamath and Jackson Counties, near the California state line, and from a few spots near the Columbia River, both in the Coast and Cascade Ranges, but not known from the remainder of Oregon. In Washington, known from the Puget Sound area, including the Olympic Peninsula, the San Juan Islands, and the lowlands east of the Sound; in British Columbia, known from southern half of Vancouver Island, north to Comox, and also from the mainland. The record from Mt. Garibaldi, collected by Virginia Anderson, is significantly north of previously recorded mainland localities.

The following locality records are in addition to those published by Bell (1970): BRITISH COLUMBIA: Goldfield (CMP); Goldstream (UK); Mount Garibaldi (UVM); Vancouver (CAS). CALIFORNIA: Denny (Bell Creek), 2500 ft. (LA); Georgetown (CAG); Happy Camp (Siskiyou Co.) (CAG); Lake Alamanor (Plumas Co.) (CAG); Maple Creek (Humboldt Co.) (CAG); Placer Co. (PU); Siskiyou Co. (MO; CNHM; BMS); Uncle Toms

(CAG); Yuba Pass (Sierra Co.) (OS; LA). OREGON: Ashland Peak, Siskiyou Mts., 7000 ft. (CNHM); Beaver-Sulfur (Jackson Co.) (OS); Forest Grove (MN); Huckleberry Mts. (Jackson Co.), 5500 ft. (CNHM); Josephine Co. (CNHM); Merlin (Josephine Co.) (OS); Oregon Caves (Jackson Co.) (CNHM).

Variation.— In most specimens from Puget Sound and vicinity, Sternum VI is impunctate in both sexes, and the submarginal groove is widely interrupted in the midline. In a few from Puget Sound, the base of Sternum VI has a few punctures. In a majority of northern females, Sternum VI is slightly impressed posteriorly. In this population the pronotum is shorter and more oblong than is usual for California specimens. Most California specimens have numerous punctures of Sternum VI, and the submarginal groove is scarcely interrupted. The female lacks an impression on Sternum VI, and the pronotum in both sexes is more slender and elongate.

These differences might indicate separate subspecies. However, it is also possible that the variation has a clinal nature. The absence of specimens from central Oregon makes it impossible to decide at present.

Bionomics.— Recorded many times from douglas-fir (*Pseudotsuga*) logs (Bell 1970).

Clinidium (*Arctoclinidium*) *valentinei* Bell 1970
(Figs. 108, 116, 122)

Clinidium (*Arctoclinidium*) *valentinei* Bell 1970: 313.

Type Material.— HOLOTYPE male, labelled: "Gorgas, Walker Co., Ala., April 17, 1949, coll. Barry Valentine" (OSU). PARATYPES one male, four females, collected with type (OSU; UVM).

Description.— Length 5.4-6.4 mm. Antennal Segments VII-X with tufts of minor setae; basal setae present on Segments VII-X; temporal lobe present; pronotum relatively short, length/greatest width 1.42; widest near middle; base, apex only slightly narrowed; lateral margins feebly curved; angular seta absent; basal impression large, 0.33 as long as pronotum, open posteriorly; outer marginal groove clearly visible in dorsal view, separated from inner groove by broad marginal carina; precoxal setae absent; sternopleural groove present.

Elytral striae broad, deep, scarcely punctate; supramarginal stria impressed in most specimens, reduced to row of coarse punctures in smallest specimens; intervals narrow, costate; intercalary stria not abbreviated posteriorly; Intervals II, III not united posteriorly; marginal stria without setae or one or two near apex; cauda of female small, rounded.

Prosternum glabrous in both sexes; metasternum not sulcate; transverse sulci of abdominal sterna narrowly separated in midline; male with median pollinose areas on Sterna I-IV, that of II narrowed anteriorly, its lateral margins straight or concave; Sternum V without pollinosity; Sternum VI of female with posterior 0.5 deeply impressed, impression bounded anteriorly by straight transverse scarp; disc with a few punctures anterior to scarp; female with large lateral pits on Sternum III; anterior trochanter of male pointed, posterior one rounded; anterior, posterior femora of male each with prominent ventral tooth; anterior tibia of male with large proximal tooth; hind calcar acute, smaller than in *C. calcaratum*, 0.40 as long as tibia.

This is the only member of the genus in the eastern U.S. to lack the median sulcus of the metasternum. The species can also be recognized by the presence of a temporal seta, though the latter is very small and often hard to see. The male is unique in the subgenus in having a ventral tooth on the posterior femur. The female resembles *C. baldufi* and *C. apertum* in having lateral pits on Sternum III but not Sternum IV. The rounded cauda separates it from *C. baldufi*, and the impression of Sternum IV from *C. apertum*.

Blanchard (1889) recognized this species as "Form B" of *C. sculptile*.

Range.— An Appalachian species, known from three widely scattered regions; north central Alabama; the mountains of eastern Tennessee, northeastern Georgia, and western North and South Carolina, and southwestern Pennsylvania, near Pittsburgh. It is not clear whether the range is really broken into relict areas or whether these merely record infrequent collection.

In addition to the localities listed by Bell (1970), we have seen specimens from the following localities: NORTH CAROLINA: Highlands (BSRI); PENNSYLVANIA: Jeanette (CMP), Wall (CMP; UVM); TENNESSEE: Chimneys C. Gr., Gt. Smoky Mt. Nat. Pk. 2800 ft. (CU), Gregory Bald, Gt. Smoky Nat. Pt. (CU); SOUTH CAROLINA: Clemson (UVM).

TABLE 1
POLYMORPHISM IN *Clinidium veneficum* LEWIS

Locality	Sex	Sternum VI	Stria III
Miyanoshita	f	b	t
Miyanoshita	m	r	s
Miyanoshita	f	l	s
Miyanoshita	f	l	s
Miyanoshita	f	b	s
Miyanoshita	m	b	s
Kiga	m	a	s
"Japan"	m	a	s
Nagasuki	m	a	s
Chiuzenji	f	b	t
Oyayama	f	b	t
Higo	f	b	t
Higo	f	b	t
Hakone	f	b	u
Mt. Kohtsu	f	a	t
Mt. Kohtsu	m	a	s
Mitsugi	m	a	s
Mitsugi	m	a	s
Mitsugi	m	a	s

(continued on next page)

Table 1 (continued)

Locality	Sex	Sternum VI	Stria III
Mitsugi	f	a	s
Mitsugi	f	a	s
"Japan"	f	b	t

Explanation of abbreviations:

Sternum VI - "b" indicates sternum tuberculate on both sides; "r" indicates tuberculate on right side only "l" indicates tuberculate on left side only "a" indicates tubercles absent.

Stria III = "t" indicates intercalary stria of both elytra contain tubercles; "u" indicates tubercle present on one side only; "s" indicates stria simple, without tubercle.

TABLE 2
COMBINATIONS OF POLYMORPHIC CHARACTERS *CLINIDIUM VENEFICUM*
LEWIS

Sternum VI	Simple Stria	Double Stria	
		Unilateral	Bilateral
bituberculate	1 m, 1 f	1 f	5 f
right tubercle	1 m	0	0
left tubercle	2 f	0	0
no tubercles	9 m, 2 f	0	1 f

m = male, f = female

TABLE 3
PROPORTION OF POPULATION WITH EACH CHARACTER STATE

I.	Sternum VI	males	females	both sexes
	bituberculate	9%	58%	34%
	right tubercle	9%	0%	4%
	left tubercle	0%	17%	9%
	no tubercles	82%	25%	53%
II.	Intercalary Stria			
	simple	100%	45.5%	70%
	unilateral double stria	0%	9%	4%
	bilateral double stria	0%	45.5%	26%

A specimen labelled (CANADA) "North West Territories, N. Karts Camp, S. Nahanni River, 61° 34' N, 124° 2' W, 28-VI-19-VIII, 1972, S. Peck, R. Syme" (BSRI) must surely be mislabelled.

Clinidium (Arctoclinidium) veneficum Lewis 1888
(Figs. 109, 110, 111)

Clinidium veneficum Lewis 1888: 83.

Clinidium (Arctoclinidium) veneficum (Lewis) Bell and Bell 1978.

Type Material.— LECTOTYPE (here designated) male, labelled: "Japan, Miyanosita, 20-XII-23-XII, 80, G. Lewis 1910-320, *Clinidium veneficum* Lewis" (BMNH). PARALECTOTYPES four females, one male, same data as lectotype (BMNH); two females, labelled: "Higo, Japan, G. Lewis" (BMNH).

Description.— Length 5.1-7.2 mm. Antennal Segments VI-X with tufts of minor setae; basal setae sparse, limited to Segments IX, X; temporal seta absent; pronotum varied in proportions, length/greatest width 1.15 to 1.55; widest near middle; base, apex nearly equally narrowed; lateral margins curved; angular seta absent; basal impressions relatively small, length about 0.25 of length of pronotum, oblique, closed posteriorly; outer marginal groove prominent in dorsal view; inner marginal groove relatively distant from it; marginal carina broad at middle, narrowed to base, apex; precoxal setae absent; sternopleural groove present.

Elytral striae broad, deep, inconspicuously punctate; elytral intervals costate; intercalary stria complete; in female, dimorphic, either doubled for short distance behind middle, isolating small tubercle which looks like remnant of additional interval, or else entire (Fig. 110); intercalary stria of male entire; supramarginal stria scarcely impressed, represented by row of punctures, abbreviated posteriorly; marginal stria impressed near apex, more anteriorly represented by row of punctures; apex of marginal stria with one or two setae, or else these setae on apical tubercle just above marginal stria; cauda dimorphic, trapezoidal in some females, rounded in others.

Prosternum glabrous in both sexes; metasternum not sulcate; transverse sulci of abdominal sterna narrowly interrupted in midline; that of Sternum II not interrupted in some females; Sterna II-V in male with median pollinose area, that of Sternum II trapezoidal; Sternum VI impressed in posterior 0.5, polymorphic, either with large tubercle near lateral margin anterior to impression on either side, or with only one such tubercle on right side, or on left side, or entirely without tubercles; female with deep lateral pits on Sternum IV; all trochanters of male rounded; anterior femur of male with small ventral tooth; hind calcar acute, narrow, rather long, about 0.33 of length of tibia, not raised above level of spurs.

This is the only member of the species known from Japan. It is similar to *C. calcaratum* of western North America, but has a broader pronotum with broader marginal carinae, and has the basal impressions closed posteriorly. It is the only member of the subgenus to have a tuft of minor setae on Antennal Segment VI.

Range.— Japan, islands of Kyushu and Honshu. On the latter island, north to Nikko. In addition to type material, we have studied the following specimens: one female, labelled: "Chiuzenju, 19, VIII-24-VIII 81, Japan, G. Lewis, 1910-330" (BMNH); one female, labelled: "Hakone, Japan, Sharp Coll. 1905-313" (BMNH); one male, labelled: "Kiga, Japan, G. Lewis, 1910-320" (BMNH); one male, labelled: "Mie Univ. Forest. Ichishi-Gun Mie, 24-VI-1956, Coll. M. Sato" (SATO); four males, two females, labelled: "Mitsugi Mura, Mie Prf., 11-VI-1956, coll. Z. Naruso" (SATO); one female, labelled: "Mt. Kohtsu (Tokushima), 31-X-1965, M. Sakai leg." (SATO); one male, labelled: "Nagasaki, Japan, G. Lewis, 1910-320, 22-V-3-VI, 81" (BMNH); one female, labelled: "Oyayama, 26-4-81, Japan, G. Lewis, 1910-320" (BMNH).

Variation.— This species exhibits remarkable polymorphism, and deserves detailed study. The intercalary stria is either entire or is divided for a short distance behind the middle, isolating a small tubercle. In all males it is entire, while the females are roughly 0.5 entire and 0.5 divided. Sternum VI is polymorphic. Many specimens have a pair of large tubercles (Fig. 111), a few have only the left tubercle, one has only the right tubercle, and many lack tubercles entirely. These forms are not secondary sexual characters, though the relative numbers of each morph are very different in the two sexes. Most males lack tubercles, while over half the females have both tubercles. The elytral cauda of the female also seems to vary in shape from a round to trapezoidal form, but detailed studies have not been completed.

The combination of characters seen in the 23 specimens which we studied are indicated in Tables 1, 2, 3. Despite the diverse appearance of the individuals, it seems likely there is one

highly polymorphic species. The lectotype is a male with the intercalary stria entire, and Sternum VI with the right tubercle, but without the left one. The other male from Miyanosima has both tubercles on Sternum VI. Thus neither agree with the majority of males, which lack both tubercles.

Bionomics.— According to Lewis (1888) this species occurs in old beech trees.

Clinidium (Arctoclinidium) baldufi Bell 1970

(Figs. 104, 113, 119)

Clinidium (Arctoclinidium) baldufi Bell 1970: 313-314.

Type Material.— HOLOTYPE male, labelled: "Dayton, Ill., May 17, 1946, coll. F. G. Werner" (MCZ 31748). PARATYPES one male, one female, same label as holotype (UVM); two males, labelled: "Lasalle Co., Ill." (MCZ); one male, labelled: "Putnam Co., Ill." (UI); two males, labelled: "Starved Rock State Park, Ill." (ISNHS).

Description.— Length 5.9-7.4 mm. Antennal Segments VII-X with tufts of minor setae; Segment VIII with basal setae few to absent; Segments IX-X with basal setae; temporal seta absent; pronotum relatively short, subquadrate, length/greatest width about 1.42; widest near middle; base, apex slightly narrowed; basal impression closed posteriorly; outer marginal groove evident in dorsal view; marginal carina relatively broad; angular seta absent; precoxal setae absent; sternopleural groove present.

Elytral striae deep, broad, inconspicuously punctate; supramarginal striae shallower than others; intervals narrow, costate; intercalary stria complete; setae absent or one or two present near tip of marginal stria; cauda of female prominent, trapezoidal.

Prosternum glabrous in both sexes; metasternum sulcate; transverse sulci rather broadly interrupted in midline; male with median pollinose areas on Sterna I-V, that of V narrowly divided in midline by glabrous carina; Sternum IV of male with median carina posterior to middle, but with pollinosity continuous anterior to carina; pollinosity of Sternum II a narrow rectangle; female with lateral pits on Sternum III; Sternum VI of female with apical 0.5 impressed.

Male with all trochanters rounded; male with small ventral tooth on anterior femur; anterior tibia of male without proximal tooth; middle, hind calcars pointed; hind one moderately large, raised slightly above level of spurs.

The male of this species resembles *C. apertum* in lacking pollinosity on the prosternum. It can be separated from the latter by the presence of a median carina on Sternum V and the absence of a proximal tooth on the anterior tibia. The female, like that of *C. apertum*, has lateral pits on Sternum III but not on Sternum IV. The female of *C. baldufi* has a prominent, trapezoidal cauda on the elytra. In both sexes, the basal impressions are closed posteriorly, while in *C. apertum* they are open.

This is probably "Form C" of *C. sculptile* according to Blanchard (1889).

Range.— More extensive and less discontinuous than indicated by Bell (1970). South to northern Florida and southern Mississippi; northeast to Delaware River Valley of New Jersey; north to vicinity of Pittsburgh, Pennsylvania, northern Illinois and central Iowa; western limit central Iowa, southeastern Missouri and northwestern Mississippi.

We have seen specimens from the following localities, in addition to those listed by Bell (1970): ALABAMA: Blount Springs (CMP), Mt. Cheaha State Park (Cleburne Co.) (TB; CAS); ILLINOIS: Crab Orchard Lake (Williamson Co.) (SI), Gorham (CAS), Olive Branch (CAS), Peoria (CNHM), Wedron (WS), Wolf Lake (Union Co.) (WRS); INDIANA: Ellettsville (Monroe Co.) (IU), Jefferson Co. (IO), Lafayette (CNHM), New Harmony (CNHM), Turkey Run State Park (Parke Co.) (CNHM; WRS); IOWA: Ames (IO), Burlington (MNH), Ledges State Park (Boone Co.) (IO); KENTUCKY: Blue Lick St. Park (Nicholas Co.) (RCG), Cumberland Falls (Whitley Co.) (UL), Hematite Lake (RCG), Henderson (WRS), Wine Spring Bald (Harlan Co.) (PA), Whitley City (McCreary Co.) (RCG); MARYLAND: Elk Neck St. Pk. (UD); MISSISSIPPI: Charleston (IO), Lucedale (CU); MISSOURI: Creve Coeur Lk. (St. Louis Co.) (MO), Cape Girardeau (MO), Reynolds Co. (MO), Rockwoods Res. (St. Louis Co.) (MO), St. Charles (CAS; UW); NEW JERSEY: Phillipsburg (CAS); NORTH CAROLINA: Black Mts. (CAS; PA), Cove Creek (Haywood Co.) (PK), Macon Co. (RCG), Wine Spring Bald (LS); OHIO: Cincinnati (CAS; UM); PENNSYLVANIA: Allegheny Co. (CMP; CU), Darby (CAS), E. Park (CAS), Easton (CAS), Ogontz (CAS), Vella Novo (Montgomery Co.) (CAS); SOUTH CAROLINA: Clemson College (WS); TENNESSEE: Blount Co., Thunderhead Mt. 6000 ft. (PA), Cades Cove, Gt. Smoky Mt. Nat. Pk., 2000 ft. (CNHM), Chimneys Campground, Gt. Smoky Mt. Nat. Pk., 2800 ft. (CU), Clarksville (UK), Gatlinburg (CNHM), Model (Stewart Co.) (DY), Newfound Gap, Gt. Smoky Mt. Nat. Pk., 5000 ft. (CU), Quinland Lk. (Putnam Co.) (TB); VIRGINIA: Nelson Co. (NMNH).

Bionomics.— Recorded from American Chestnut, and white oak logs (Bell 1970).

Clinidium (Arctoclinidium) apertum Reitter 1880

Clinidium apertum Reitter 1880: 29-30.

Clinidium (Arctoclinidium) allegheniense georgicum Bell and Bell 1975.

Clinidium (Arctoclinidium) apertum (Reitter) Bell and Bell 1978.

Type Material.— (*apertum*) HOLOTYPE male, labelled: "Himalaya, *Clinidium apertum* India, Reitt." (with red "typus" label) (NMW). The locality data on this specimen must be erroneous; (*georgicum*) HOLOTYPE male, labelled: "GEORGIA, Cartersville, 26-III-39, P. W. Fattig" (NMNH); PARATYPES one male, same data as holotype (GA); two females, same data as holotype (CNHM); one male, labelled "Athens, Georgia, 6-X-54, K. Parrish" (GA); two males, labelled "West Pace's Ferry X, Marietta Hgy (DeKalb Co.), 12-IX-54, W. H. Cross" (UVM); one female, labelled: "Dallas, 16-IV-44, P. W. Fattig" (UVM).

Description.— Length 5.5-7.0 mm. Antennal Segments VII-X with tufts of minor setae; basal setae present on Segments VII-X or VIII-X; temporal seta absent; pronotum moderately long, length/greatest width about 1.48; widest near middle, base scarcely narrowed, apex moderately so; basal impressions oblique, relatively long, about 0.38 of length of pronotum, widely open posteriorly; outer marginal groove clearly visible in dorsal view; marginal carina relatively broad; angular seta, precoxal setae absent; sternopleural groove present.

Elytral striae deep, broad, inconspicuously punctate; supramarginal stria shallower than the others; intervals narrow, costate; intercalary stria complete; setae absent or one or two present near apex of marginal stria; cauda of female elytra very small, rounded.

Prosternum glabrous in both sexes; metasternum sulcate; transverse sulci rather narrowly interrupted in midline; male with median pollinose areas on Sterna II-IV, in some specimens also on Sternum V, latter not carinate; pollinosity of Sternum II resembling letter "T", or with stem of "T" disconnected or absent, leaving curved transverse bar; female with lateral pits on Sternum III; Sternum VI not impressed; male with all trochanters rounded, anterior femur with large but obtuse ventral tooth, anterior tibia with large but obtuse proximal tooth; middle calcar narrow, pointed; hind calcar triangular, acute, not raised above level of spurs, much smaller than in *C. baldufi*.

The broadly open basal impressions will separate this species from all others of the eastern U.S. except for *C. valentinei* (and some specimens of *rosenbergi*). The sulcate metasternum separates it from *valentinei*. The male resembles *C. baldufi* in lacking pollinosity on the prosternum, but differs in having a proximal tooth on the anterior tibia, in lacking the median carina on Sternum V, and in having a smaller hind calcar. The female resembles *C. baldufi* and *C. valentinei* in having pits in Sternum III but not Sternum IV. It differs from the former in having a rounded cauda, and from the latter in lacking an impression on Sternum VI.

This species is divided into two subspecies, separated on the presence or absence of a median pollinose area on Sternum V of the male. An isolated female specimen labelled "Mobile, Loding" (MCZ) from Southern Alabama, cannot be identified to subspecies.

Clinidium (Arctoclinidium) apertum apertum Reitter 1880
(Figs. 114, 120)

Clinidium apertum Reitter 1880: 29-30.

Clinidium (Arctoclinidium) allegheniense georgicum Bell and Bell 1975.

Clinidium (Arctoclinidium) apertum apertum (Reitter) Bell and Bell 1978.

Description.— Male without median pollinose area on Sternum V; pollinosity of Sternum II of male in most specimens forming a broken "T", in a few (including holotype of *C. apertum*), an unbroken "T", in a few a curved transverse bar, stem of "T" entirely absent.

Range.— Mountains of northern Georgia, recorded only from the type series.

Clinidium (Arctoclinidium) apertum allegheniense Bell and Bell 1975

Clinidium allegheniense allegheniense Bell and Bell 1975: 65-66.

Clinidium apertum allegheniense Bell and Bell 1978.

Type Material.— HOLOTYPE male, labelled: "Allegheny, 1-VI-24, coll. Chermock" (UK). This locality is now the Northside district of Pittsburgh. PARATYPES two females, same data as holotype (UK); one male, one female, same data (MCZ); 13 males, two females, labelled "PENNSYLVANIA: Wall, VI-21, H. Klages Collection" (CMP).

Description.— As described for *C. apertum* s. str., except that median pollinose area is present on Sternum V.

Range.— Southwestern Pennsylvania, and possibly mountains of western North Carolina. In addition to the type series, we have studied the following additional specimens from Pennsylvania: one male, one female, labelled: "Squaw's Run, Pa. i-VI-24, coll. Chermock, L. J. Milne collection" (UNH). We provisionally assigned the following specimens from western North Carolina to this subspecies; one male, two females, labelled: "Mount Mitchell, Black Mts., North Carolina" (CAS). These specimens have the median pollinose area on Sternum V as in *C. allegheniense*. They are atypical in having the inner impression of Sternum VI longer and more deeply impressed, and in the male, the stem of the "T" is dilated posteriorly.

Clinidium (Arctoclinidium) rosenbergi Bell 1970

(Figs. 103, 112, 118)

Rhysodes sculptilis Newman 1838: 666 (*partim*)

Clinidium (Arctoclinidium) rosenbergi Bell 1970: 315-316.

Type Material.— HOLOTYPE male, labelled: "Turkey Run State Park, Parke Co., Indiana, May 13, 1950, coll. Ross T. Bell" (MCZ 31749). PARATYPES one female, same data as holotype (UVM); one male, same locality, coll. Buser, May 3, 1953 (UI); three females, labelled: "Parke County, Indiana, coll. N. M. Downie, May 8, 1965" (WR).

Description.— Length 6.2-7.8 mm. Antennal Segments VII-X with tufts of minor setae; basal setae present on Segments VII-X or VIII-X; temporal seta absent; pronotum moderately long, length/greatest width 1.44; widest near middle, sides nearly parallel to weakly curved; basal impression closed posteriorly (open in a few specimens); outer marginal groove evident in dorsal view; marginal carina relatively broad; angular seta, precoxal seta absent; sternopleural groove present.

Elytral striae deep, broad, inconspicuously punctate; supramarginal stria shallower than the others; intervals narrow, costate; intercalary stria complete; setae absent or one or two present in or just above apex of marginal stria; cauda of female small, rounded.

Prosternum of male with medial pollinose area; metasternum sulcate; male with median pollinose areas on Sterna I-IV, median area of Sternum V glabrous; pollinose area of Sternum II relatively broad, constricted near middle, apex, base equally broad; female with lateral pits on Sternum III, IV equally large; Sternum VI impressed in some female specimens, not impressed in other ones.

Male with all trochanters rounded; anterior femur of male with ventral tooth; anterior tibia of male with strong angle proximad to cleaning organ, representing poorly defined proximal tooth; calcars pointed; hind one very small, scarcely longer than middle one.

Males from this species resemble those of *C. sculptile* in having a median pollinose area on the prosternum, but lack pollinosity at the middle of Sternum V and have a very small hind calcar. Females have equally large lateral pits in Sterna III and IV, while in *C. sculptile* the pits of Sternum IV are smaller than those of III.

Range.— North to the Great Lakes in Pennsylvania, Ohio, and Indiana. West to the Mississippi River in Tennessee and southern Illinois, and slightly west of the river near St. Louis, Missouri. South to southwestern Tennessee and western North Carolina. East to the Delaware River in Pennsylvania, but not known from east of the Appalachians south of Pennsylvania. Bell (1970) discussed female specimen from Mobile, Alabama, which may be this species, though the shape of the pronotum is unusual. It might be a distinct, though closely related species, but males must be collected to be sure of its status. A specimen labelled: "Treesbank, Manitoba" (BSRI) is likely to have an incorrect locality label.

We have studied the following specimens in addition to those listed by Bell (1970): ILLINOIS: Wolf Lake (Union Co.) (WRS); INDIANA: Lafayette (CNHM); KENTUCKY: Anchorage (UL), Mammoth Cave N. Park (WRS), Wolf Creek (Wayne Co.) (UL); MISSOURI: St. Charles (UW); OHIO: Cincinnati (UM), Clermont Co. (UM), Cleveland (HL), Columbiana Co. (UD), Oxford (NC); PENNSYLVANIA: Blain (AP), Harmerville (CMP), Jeanette (CMP).

Variation.— This species will merit additional study when more material is available. Sternum VI is not at all impressed in some specimens, mostly from western parts of the range, but is deeply impressed in others, especially ones from eastern localities. There is also considerable variation in the shape of the pronotum. Most specimens from Kentucky have a subquadrate pronotum with the sides nearly parallel. In specimens from other regions, the base and apex of the pronotum are more narrowed.

Clinidium (Arctoclinidium) sculptile (Newman) 1838
(Figs. 115, 121)

Rhysodes sculptilis Newman 1838: 666 (*partim*)

Clinidium sculptile (Newman) Chevrolat 1873a.

Clinidium (Arctoclinidium) sculptile (Newman) Bell 1970.

Type Material.— LECTOTYPE male, labelled: "Wheeling, Virginia" (BMNH). This locality is now in West Virginia. PARALECTOTYPES: Newman listed two localities, Wheeling and Mount Pleasant, Ohio. The latter was represented by two females. One of these is not conspecific with the male, but are the species described by Bell as *C. rosenbergi*, while the other is conspecific with the holotype.

Description.— Length 6.5-7.6 mm. Antennal Segments VII-X with tufts of minor setae; basal setae present on Segments VII-X or VIII-X; temporal seta absent; pronotum moderately long, length/greatest width about 1.45; pronotum subquadrate, lateral margins nearly parallel; basal impression closed posteriorly; outer marginal groove evident in dorsal view; marginal carina relatively broad; angular seta, precoxal setae absent; sternopleural groove present.

Elytral striae deep, broad, inconspicuously punctate; supramarginal stria impressed, shallower than the others; intervals narrow, costate; intercalary stria complete; setae absent or one or two present in or just above apex of marginal stria; cauda of female prominent, rounded.

Prosternum of male with median pollinose area; metasternum sulcate; male with median pollinose areas on Sterna II-V; pollinosity of Sternum II constricted near middle, anterior margin broader than posterior one; female with large lateral pits on Sternum III, smaller ones on Sternum IV; Sternum VI of female impressed in apical 0.5.

Male with all trochanters rounded; anterior femur of male with very small, obtuse ventral tooth or angle; anterior tibia of male with small, indistinct angle in place of proximal tooth; calcars pointed; hind calcar rather large, about 1.3 longer than middle one.

Males of *C. sculptile* resemble those of *C. rosenbergi*, in having a median pollinose area on the prosternum, but differ from the latter species in having median pollinosity on Sternum V and in having a larger hind calcar. Females differ from all other members of the subgenus in having large lateral pits on Sternum III and smaller ones on Sternum IV.

Range.— More extensive than supposed by Bell (1970). Primarily Appalachian from north central Alabama to southern New York (Catskill Mts.), but also in the Piedmont from northern Virginia northwards. Midwestern records are from central Kentucky, southern Ohio and Indiana, and the vicinity of Saint Louis, Missouri. *C. sculptile* is the commonest member of the genus in the eastern part of its range, but is much rarer than *C. baldufi* and *C. rosenbergi* in the Midwest. There are several specimens labelled as coming from localities far beyond the range as described below. Among these are some from unspecified localities in Florida (MO) and Texas (CAS), and from Westview, Millvale, and Squaw's River, in Manitoba (BSRI). We regard these records as dubious.

We have studied specimens from the following localities in addition to those listed by Bell (1970): ALABAMA: Sawdust (WRS); DELAWARE: Newark (UD); DISTRICT OF COLUMBIA: Rock Creek Park (AU); GEORGIA: Athens (UW), Clayton 2000-3700 ft. (CAS; CNHM; BMS); INDIANA: Turkey Run Park (Parke Co.) (CNHM); KENTUCKY: Mammoth Cave Nat. Park (TB); MARYLAND: Elk Neck St. Park (UT; UD), Forest Glen (NMNH; AU), Glen Echo (Montgomery Co.) (WRS), Catoctin Mtn. (Frederick Co.) (AU); MISSOURI: St. Charles (UW), St. Louis (CU); NEW JERSEY: "N. J." (CAS; CNHM); NORTH CAROLINA: Blue Ridge (LUN), Transylvania Co. (RCG); OHIO: Cincinnati (CAS); PENNSYLVANIA: Allegheny (CMP; MO), Bethayres (UW), Cook Forest (UVM), Cooksburg (WS), Charter Oak (AP), Harrisburg (SDA; AP), Ingelnook (AP), Jeanette (CMP), Keystone St. Pk. (WRS), Montebello (AP), Rockville (CU; CAS; AP); SOUTH CAROLINA: Oconee Co. (CAS; WRS); TENNESSEE: Cades Cove, Great Smoky Mts. Nat., Pk. 2000' (CNHM); VIRGINIA: Brush Mts. (Montgomery Co.)

(VP), Potomac River (Fairfax Co.) (CAS), Turkey Run, McLean (UVM); WEST VIRGINIA: Burlington (Mineral Co.) (CMP), White Sulphur (CNHM).

Bionomics.— Recorded from pitch pine and tulip-tree (*Liriodendron*) Bell (1970).

SUBGENUS *CLINIDIUM SENSU STRICTO*

Type species.— *Clinidium guildingii* Kirby.

Description.— Antennal stylet relatively large; tufts of minor setae present on Segments IV-X, V-X, VI-X, or VII-X, or else minor setae entirely absent except for Segment XI; temporal setae one to four; eye very narrowly crescentic in most species, in a few species minute, round, resembling an ocellus, or bilobed, or divided into two ocellus-like parts, or large, hemispherical. In many species, completely pigmented in some, probably old individuals; marginal groove of pronotum single; pronotum with angular seta, and one or more marginals; in some species, also with discal or basal setae; sternopleural grooves absent; elytral striation incomplete; marginal stria fourth or fifth from suture; supramarginal seta absent; inner elytral intervals flat to convex, not carinate; elytral setae numerous in most species; metasternum with or without median sulcus; base of anterior tarsus opposite cleaning organ.

The reduced striation makes this subgenus similar to *Tainoa*, from which it is distinguished by the position of the cleaning organ and the complete parasutural stria which is not abbreviated anteriorly.

The subgenus is large and the species are quite varied in appearance. Probably it is restricted to the Neotropical Realm, from Guatemala southwards in Central America, and in the Andean Region south to Ecuador. The only records from the Amazon Basin are from the upper or western portion, while the easternmost record from the northern coast is from Cayenne. The subgenus is widely distributed also in the Greater and Lesser Antilles.

Two of the four species of the *C. beccarii* group, *C. beccarii* and *C. argus*, are recorded from Old World localities, the former species from New Guinea and the latter from the Philippines. Each is known from only one specimen, and we suspect that both are mislabelled, as they are closely related to Central American species.

Phylogeny.— We divide the subgenus into six species groups, most of which are probably monophyletic. Possible exceptions are noted in the discussions of the groups in question.

- I. *impressum* group. Tufts of minor setae on Antennal Segments IV-X; eye large, broadly oval; temporal, pronotal setae absent. One species. This group might really belong to *Rhyzodiastes*, and have secondarily lost the anterior part of the paramedian groove.
- II. *granatense* group. Tufts of minor setae VII-X. Three species.
- III. *insigne* group. Tufts of minor setae VI-X. Four species.
- IV. *guildingii* group. Tufts of minor setae on Segments V-X; anterior median pit very small. 25 species.
- V. *cavicolle* group. Tufts of minor setae V-X; anterior median pit greatly enlarged. Nine species.
- VI. *beccarii* group. Tufts of minor setae absent; eye constricted or divided. Four species.

KEY TO SPECIES

- 1 Eye large, broadly oval; median groove of pronotum with middle 0.33 dilated, separated by constriction from anterior median pit; temporal, pronotal setae absent (*impressum* group)

C. impressum new species, p. 99

- 1' Eye small, narrowly crescentic, or constricted, or ocelliform, or divided; median groove not dilated; temporal, pronotal setae present 2
- 2 (1') Outer antennal segments with tufts of minor setae on Segments V-X, VI-X, or VII-X; eye narrowly crescentic or ocelliform (may be concealed by heavy pigmentation) 3
- 2' Outer antennal segments without tufts of minor setae; eye bilobed or divided (*beccarii* group) 43
- 3 (2) Tufts of minor setae present on Antennal Segments VI-X or VII-X, but absent from Segment V 4
- 3' Tufts of minor setae present on Antennal Segments V-X 10
- 4 (3) Tufts of minor setae present on Segments VII-X, but absent from Segment VI (*granatense* group) 5
- 4' Tufts of minor setae present on Segments VI-X (*insigne* group) 7
- 5 (4) Eye narrowly crescentic; metasternum sulcate; head as wide as long; one temporal seta; pronotum with one angular seta and without or with one marginal seta, near angular; otherwise without pronotal setae; male without proximal tooth on anterior tibia; male calcars triangular, not notched above; female (where known) with lateral pits in Sternum III and IV. Anterior median pit less enlarged 6
- 5' Eye small, round, ocelliform; metasternum not sulcate; head longer than wide; two temporal setae; pronotum with one angular, two marginals, anterior to middle, one basal, two discal setae; male with proximal tooth on anterior tibia; male calcars notched above; female with lateral pits on Sternum IV, not III; anterior median pit very large *C. incudis* Bell, p. 114
- 6 (5) Intercalary stria complete; one marginal seta on pronotum; transverse sulcus of Sternum V nearly complete in male; middle calcar obliquely truncate at tip *C. hammondi* new species, p. 113
- 6' Intercalary stria abbreviated; marginal seta absent; transverse sulcus of male Sternum V broadly interrupted; middle calcar acutely pointed. *C. granatense* Chevrolat, p. 113
- 7 (4') Temporal lobes convergent posteriorly; anterior median pit of pronotum small to obsolete; antennal stylet very small; male protibia without proximal tooth 8
- 7' Temporal lobes divergent posteriorly; anterior median pit very large, with tubercle; antennal stylet very large; male protibia with proximal tooth (metasternum sulcate; intercalary stria abbreviated posteriorly) *C. dubium* Grouvelle, p. 115
- 8 (7) Metasternum with median sulcus; intercalary stria abbreviated posteriorly 9
- 8' Metasternum not sulcate; intercalary stria entire *C. boroquense* Bell, p. 117
- 9 (8) Preapical tubercles truncate, medial angles of tubercles well separate; head flattened, as wide as long; parasutural stria without setae *C. insigne* Grouvelle, p. 115
- 9' Preapical tubercles sinuate, medial angles lobate; head convex, longer than wide; parasutural stria with many setae

 <i>C. howdenorum</i> new species, p. 116	
10 (3')	Anterior median pit of pronotum very small, not wider than median groove (<i>guldinii</i> group)	11
10'	Anterior median pit very large, much broader than median groove (<i>cavicollae</i> group)	35
11 (10)	Intercalary stria entire; pronotum with discal seta	12
11'	Intercalary stria abbreviated, ending blindly posteriorly; pronotum without discal setae	28
12 (11)	Apex of intratubercular stria impressed, apical, preapical tubercles distinct	13
12'	Apex of intratubercular stria not impressed; preapical, apical tubercles not separated	24
13 (12)	Paramedian groove (basal impression plus discal striole), 0.6–0.9 of length of pronotum	14
13'	Paramedian groove 0.5 or less of length of pronotum	15
14 (13)	Paramedian groove about 0.9 of length of pronotum; preapical tubercle angulate posteriorly, angle overhanging subapical space	
 <i>C. integrum</i> Grouvelle, p. 119	
14'	Paramedian groove about 0.6 of length of pronotum; preapical tubercle not angulate nor overhanging subapical space	
 <i>C. pilosum</i> Grouvelle, p. 119	
15 (13')	Median lobe joined laterally to antennal lobes; frontal grooves not joined to tentorial pits	16
15'	Median lobe not joined laterally to antennal lobes; frontal grooves joined to tentorial pits	18
16 (15)	Precoxal seta absent	17
16'	Precoxal seta present	
 <i>C. alleni</i> new species, p. 122	
17 (16)	Median lobe short, ending opposite anterior or mid level of eye; paramedian groove 0.5 length of pronotum	
 <i>C. whiteheadi</i> new species, p. 122	
17'	Median lobe longer, ending posterior to mid level of eye; paramedian groove short, 0.2 length of pronotum	
 <i>C. haitiense</i> Bell, p. 125	
18 (15')	Precoxal seta present	19
18'	Precoxal seta absent	21
19 (18)	Elytral humeri strongly narrowed; metasternum with deep median sulcus	
 <i>C. oberthueri</i> Grouvelle, p. 121	
19'	Elytral humeri weakly narrowed; median sulcus of metasternum very shallow to absent	20
20 (19')	Discal striole of pronotum present; eye elongate	
 <i>C. humboldti</i> new species, p. 123	
20'	Discal striole absent; eye very small, short	
 <i>C. trionyx</i> new species, p. 124	
21 (18')	Parasutural stria with complete series of setae; paramedian groove about 0.5 of length of pronotum	
 <i>C. jolyi</i> new species, p. 120	
21'	Parasutural stria without setae; paramedian groove 0.3 or less of length of pronotum	22
22 (21')	Median lobe elongate, extending posterior to middle of eye; frontal grooves	

- deep, narrow, both margins equally sharp, both conspicuously pollinose . . .
C. corbis Bell, p. 126
- 22' Median lobe short, ending opposite anterior part of eye; frontal grooves shallow, lateral margin indistinct, margins not or but faintly pollinose . . . 23
- 23 (22') Sutural interval narrow, convex; female with lateral pits distinct . . .
C. jamaicense Arrow, p. 128
- 23' Sutural interval broad, flat; female with lateral pits indistinct . . .
C. chiolinoi Bell, p. 128
- 24 (12') Metasternum with median sulcus; three or four temporal setae; occipital setae absent . . . 25
- 24' Metasternum without median sulcus; one temporal seta; one pair of crossed occipital setae . . . *C. rossi* Bell, p. 129
- 25 (24) Median lobe joined to antennal lobe; discal striole absent; precoxal setae absent . . . *C. penicillatum* new species, p. 131
- 25' Median lobe separate from antennal lobe; discal striole present; precoxal setae present . . . 26
- 26 (25') Antennal stylet very short, acute; subapical, apical tubercles one continuous elongated lobe; median sulcus narrow . . . 27
- 26' Antennal stylet long, slender, acute; tip of subapical tubercle abrupt, truncate, not continuous with apical tubercle; median sulcus wider . . .
C. kochalkai new species, p. 132
- 27 (26) Intratubercular stria entire, thin, pilose line anterior to tubercular punctures; frontal groove deeper; median lobe narrower . . .
C. segne new species, p. 131
- 27' Intratubercular stria abbreviated from tubercular punctures; frontal groove shallow, median lobe wider . . . *C. dormans* new species, p. 130
- 28 (11') Metasternum without median sulcus; male without proximal tooth on anterior tibia; middle, hind tibiae with false spurs (West Indian species) . . . 29
- 28' Metasternum with median sulcus; male with proximal tooth on anterior tibia; false spurs absent (South American species) . . . 32
- 29 (28) Apical tubercles barely touching in midline above a large space; female with median tubercles on Sternum VI; discal striole 0.5 as long as pronotum; temporal setae two to four . . . *C. guildingii* Kirby, p. 133
- 29' Apical tubercles broadly contiguous in midline, without conspicuous space below them; female (where known) with transverse scarp on Sternum VI; discal striole in most specimens less than 0.5 of length of pronotum; two temporal setae . . . 30
- 30 (29') Intratubercular stria not impressed, represented only by row of fine punctures; marginal stria incomplete anteriorly; male with ventral surface of anterior femur with many tubercles; calcars not angulate dorsally (female unknown) . . . *C. microfossatum* new species, p. 134
- 30' Intratubercular stria, marginal stria impressed, complete; male without ventral tubercles on anterior tibia; calcars angulate dorsally; female with transverse scarp on Sternum VI . . . 31
- 31 (30') Basal impression plus discal striole 0.35 to 0.40 of length of pronotum; calcars weakly angulate dorsally; female with shallow impression posterior

- to scarp of Sternum VI, forming obtuse angle in lateral view; impression convex, glabrous in midline, with oval pollinose concavity on either side *C. smithsonianum* new species, p. 134
- 31' Basal impression plus discal striole 0.25 or less of length of pronotum; calcars strongly angulate dorsally; female with deep impression posterior to scarp of Sternum VI, forming right angle in lateral view; impression entirely pollinose *C. planum* (Chevrolat), p. 135
- 32 (28') Female with Sternum VI deeply impressed in posterior 0.33, with pair of notches defining median lobe (male unknown) 33
- 32' Female with Sternum VI not impressed 34
- 33 (32) Parasutural stria without setae; median lobe of Sternum VI of female narrow, trapezoidal *C. pala* new species, p. 139
- 33' Parasutural stria with several setae; median lobe of Sternum VI of female broad, rectangular *C. excavatum* new species, 138
- 34 (32') Parasutural stria without setae; frontal space entirely pollinose; male with calcars acute, proximal tibial tooth acute *C. rojasi* Chevrolat, p. 136
- 34' Parasutural stria with three or four setae; frontal space glabrous in middle; male with calcars obtuse, proximal tooth of anterior tibia represented by obtuse angle *C. bechyneorum* new species, p. 138
- 35 (10') Intercalary stria entire; anterior median pit with central tubercle 36
- 35' Intercalary stria abbreviated posteriorly; anterior median pit without median tubercle *C. mathani* Grouvelle, p. 140
- 36 (35) Metasternum without median sulcus *C. humile* new species, p. 140
- 36' Metasternum with median sulcus 37
- 37 (36') Disc of temporal lobe without isolated or semi-isolated setiferous puncture; notopleural suture without pollinosity 38
- 37' Disc of temporal lobe with one large setiferous puncture, either isolated or in narrow contact with posterior pilosity; notopleural suture with pollinosity . . . 41
- 38 (37) Basal impression plus discal striole 0.5 or less of length of pronotum; antennal stylet long 39
- 38' Basal impression plus discal striole more than 0.5 of length of pronotum; antennal stylet short 40
- 39 (38) Discal striole 0.45 of length of pronotum, curved; margin of median groove curved evenly into anterior median pit; basal setae absent *C. curvatum* new species, p. 141
- 39' Discal striole 0.20 of length of pronotum, scarcely curved; margin of median groove sinuate opposite tubercle, latter compressed *C. foveolatum* Grouvelle, p. 142
- 40 (38') Dorsal surface of femora glabrous, anterior median pit closed anteriorly, round; female with transverse sulci of all sterna broadly interrupted in midline; Sternum VI of female with submarginal groove reaching nearly to anterior margin *C. cavicolle* Chevrolat, p. 142
- 40' Dorsal surface of femora pilose; anterior median pit open anteriorly, sinuate laterally; sterna of female with transverse sulci narrowly interrupted in midline; Sternum VI of female with submarginal groove not extending anterior to middle *C. crater* new species, p. 143

- 41 (37') Margin of median groove curved evenly into that of anterior median pit; basal impression plus discal striole 0.30 of length of pronotum; discal seta of temporal lobe in isolated pollinose puncture in most specimens anterior to hind margin of eye *C. centrale* Grouvelle, p. 144
- 41' Margin of median groove sinuate near anterior median pit; basal impression plus discal striole 0.45 or more of length of pronotum; discal seta of temporal lobe at or posterior to posterior margin of eye, narrowly contacting pilosity of occiput 42
- 42 (41') Margin of median groove shallowly sinuate posterior to tubercle of anterior median pit, nearly oblique; basal impression plus discal striole about 0.55 of length of pronotum *C. validum* Grouvelle, p. 144
- 42' Margin of median groove strongly emarginate posterior to tubercle; basal impression plus discal striole about 0.45 of length of pronotum *C. spatulatum* new species, p. 145
- 43 (2') Eye constricted but not divided; median groove narrow, much narrower than anterior median pit; sternopleural groove incomplete; postantennal groove narrowly pollinose 44
- 43' Eye divided into two ocellus-like organs; median groove very broad, as broad as anterior median pit; postantennal groove broadly pollinose; sternopleural groove complete 45
- 44 (43) Median groove of pronotum closed posteriorly, slightly constricted at midpoint; posterior 0.5 of sternopleural groove marked by three separate pilose spots; male with pair of tubercles on either side of midline on abdominal Sterna III, IV; transverse sulci of male with only traces of pollinosity, but with pits at medial ends *C. moldenkei* new species, p. 146
- 44' Median groove broadly open posteriorly, not constricted at middle; posterior 0.5 of sternopleural groove continuously pollinose; male with deep longitudinal groove at middle of Sterna I-III, shallower one on Sternum IV; no tubercles on Sterna III, IV; transverse sulci of male abdomen pollinose, interrupted at midline *C. sulcigaster* Bell, p. 147
- 45 (43') Paramedian grooves about 0.5 of length of pronotum; male with middle, hind calcars cultrate; pollinosity of Sterna II, III extending anteriorly onto medial part of Sternum I *C. argus* new species, p. 148
- 45' Paramedian grooves over 0.67 of length of pronotum; male with middle, hind calcars triangular; Sternum III with transverse pollinose band, not extending anteriorly to Sternum I *C. beccarii* Grouvelle, p. 148

THE IMPRESSUM GROUP

This group is characterized by the large, almost round eyes, and the absence of temporal and pronotal setae. The median groove is dilated in the middle portion, and the dilation is separated from the anterior median pit by a constriction. A very small tuft of minor setae is present on Segment IV of the antenna, and a larger one on Segment V. The intercalary stria is complete, while the intratubercular stria is abbreviated posteriorly.

The large eyes are unique within the genus, and are reminiscent of those of *Rhyzodiastes* subgenus *Rhyzostrix*. The dilation of the median groove is similar to that of *Clinidium kochalkai*, but in the latter species the anterior median tubercle is not enlarged, the eyes are small and narrow, and temporal and pronotal setae are present. Only one species belongs to this group.

Clinidium (sensu stricto) impressum new species

(Fig. 124)

Type Material.— HOLOTYPE male, labelled: "Guyane Franc., St. Laurent du Maroni, colln. Le Moul, *Clinidium impressum* Grouv." (MNHN). The latter name was never published. Segments VI-XI of the antenna are missing from the holotype.

Description.— Length 5.3 mm. Antennal Segment IV with small tuft of minor setae; Segment V with larger one; Segments VI-XI missing from holotype; Segments III-V each with subapical ring of pollinosity; head slightly longer than wide; frontal grooves shallow, linear, not pollinose; median lobe triangular, tip pointed, opposite middle of eye; frontal space very narrow; temporal lobe rounded, nearly glabrous, small, finely pollinose area near posterior margin; eye large, nearly round, but short, less than 0.33 of length of temporal lobe; orbital groove absent; temporal setae absent; one pair of postlabial setae.

Pronotum elongate, oval, length/greatest width 1.61, widest near middle, sides strongly curved, apex, base strongly narrowed, rounded; median groove narrowly dilated, separated from median pits by constrictions; anterior median pit large, round; posterior median pit narrow, elongate; basal impression open posteriorly, tapered anteriorly, preceded by very short discal striole; combined length of basal impression, discal striole about 0.25 of length of pronotum; marginal groove very narrow, invisible in dorsal view; pronotal setae absent; notopleural suture glabrous; sternopleural groove absent; precoxal setae absent.

Elytra rather elongate; sutural interval nearly flat; Intervals II, III convex; sutural stria impressed, punctured, complete; parasutural impressed, punctate, complete; intercalary impressed, punctures complete, joining parasutural posteriorly; intratubercular effaced near base, for most of length not impressed, represented by row of punctures, slightly impressed near apex, but apex effaced, preapical tubercle therefore not distinct from apical tubercle; apical tubercles inflated, truncate posteriorly, nearly contiguous in midline; marginal stria entire, impressed, punctate; sutural stria with one seta near apex; intercalary stria with five setae in complete row; intratubercular stria with five setae near apex, in row of punctures on lateral face of apical tubercle; marginal stria eight or nine in complete row; metasternum not sulcate; male with transverse sulci complete on Sterna III, IV, narrowly interrupted on Sternum V; Sternum IV of male with small, round lateral pit; Sternum VI of male without transverse sulci, but with short submarginal sulcus, one pair of setae; male without ventral tooth on anterior femur, without proximal tooth; calcaria small, blunt; middle, hind tibiae with two equal spurs, without false spurs; female unknown.

THE *GRANATENSE* GROUP

This group contains species in which tufts of minor setae are restricted to Antennal Segments VII-X. There is one pair of postlabial setae. The anterior median pit is expanded, several times wider than the median groove, but is not tuberculate. The paramedian grooves are about 0.5 as long as pronotum. The sternopleural groove is present. In the species in which the female is known, Sternum VI of the female has a median pit. The eye is either narrowly crescentic or is ocelliform. This group contains three species, two from northern Colombia, and the third from Puerto Rico.

Phylogeny.— *C. granatense* and *C. hammondi* share several characters, including the presence of a metasternal sulcus and a proximal tooth on anterior tibia of the male, indicating that they are closer to one another than to *C. incudis*. The presence of a median pit on Sternum VI of the female in the latter species suggests a real relationship with the Colombian species, rather than just a coincidence in the arrangement of tufts of minor setae.

Plate 11. Figs. 124–137. Subgenus *Clinidium sensu stricto*. Figs. 124–131. Head and pronotum, dorsal aspect; Fig. 124, *C. (s. str.) impressum* new species; Fig. 125, *C. (s. str.) hammondi* new species; Fig. 126, *C. (s. str.) granatense* Chevrolat; Fig. 127, *C. (s. str.) incudis* Bell; Fig. 128, *C. (s. str.) dubium* Grouvelle; Fig. 129, *C. (s. str.) boroquense* Bell; Fig. 130, *C. (s. str.) howdenorum* new species; Fig. 131, *C. (s. str.) insigne* Grouvelle; Fig. 132, Head, left lateral aspect, *C. (s. str.) incudis* Bell; Figs. 133–134, Left elytron, dorsal aspect; Fig. 133, *C. (s. str.) hammondi* new species; Fig. 134, *C. (s. str.) granatense* Chevrolat; Figs. 135–136, Sterna IV–VI, right half; Fig. 135, *C. (s. str.) insigne* Grouvelle; Fig. 136, *C. (s. str.) insigne* Grouvelle (Cali specimen); Fig. 137, Left elytron, apex, dorsal aspect, *C. (s. str.) howdenorum* new species.

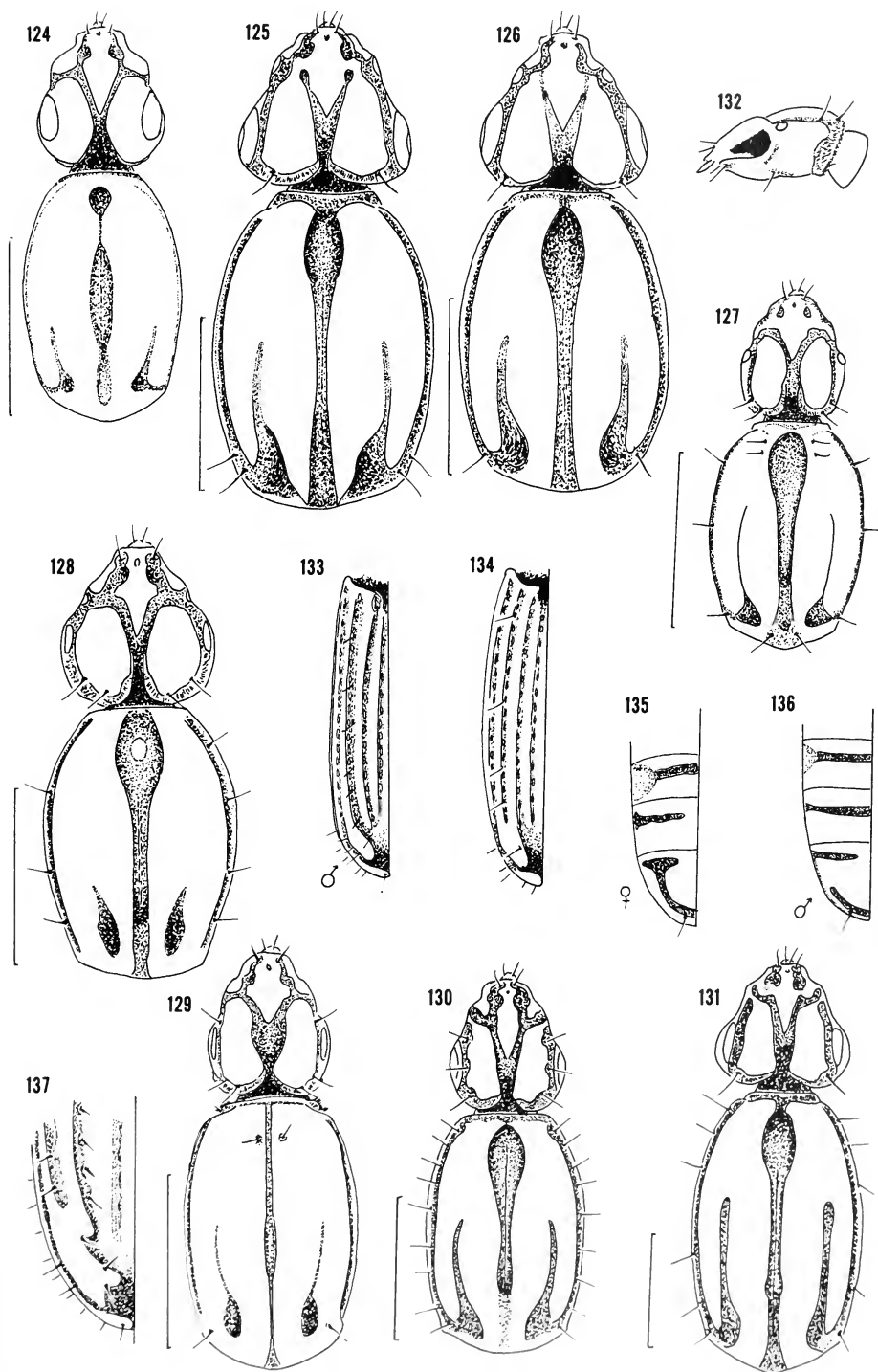


Plate 12. Figs. 138–150. Subgenus *Clinidium sensu stricto*. Figs. 138–144, Head and pronotum, dorsal aspect; Fig. 138, *C. (s. str.) integrum* Grouvelle; Fig. 139, *C. (s. str.) pilosum* Grouvelle; Fig. 140, *C. (s. str.) jolyi* new species; Fig. 141, *C. (s. str.) oberthueri* Grouvelle; Fig. 142, *C. (s. str.) alleni* new species; Fig. 143, *C. (s. str.) whiteheadi* new species; Fig. 144, *C. (s. str.) humboldti* new species; Fig. 145, Right elytron, apex, posterior aspect, *C. (s. str.) integrum* Grouvelle; Figs. 146–148, Sterna V–VI, right half; Fig. 146, *C. (s. str.) pilosum* Grouvelle, female; Fig. 147, *C. (s. str.) jolyi* new species, female; Fig. 148, *C. (s. str.) alleni* new species; Figs. 149–150, Left elytron, apex, dorsal aspect; Fig. 149, *C. (s. str.) alleni* new species; Fig. 150, *C. (s. str.) humboldti* new species, female.

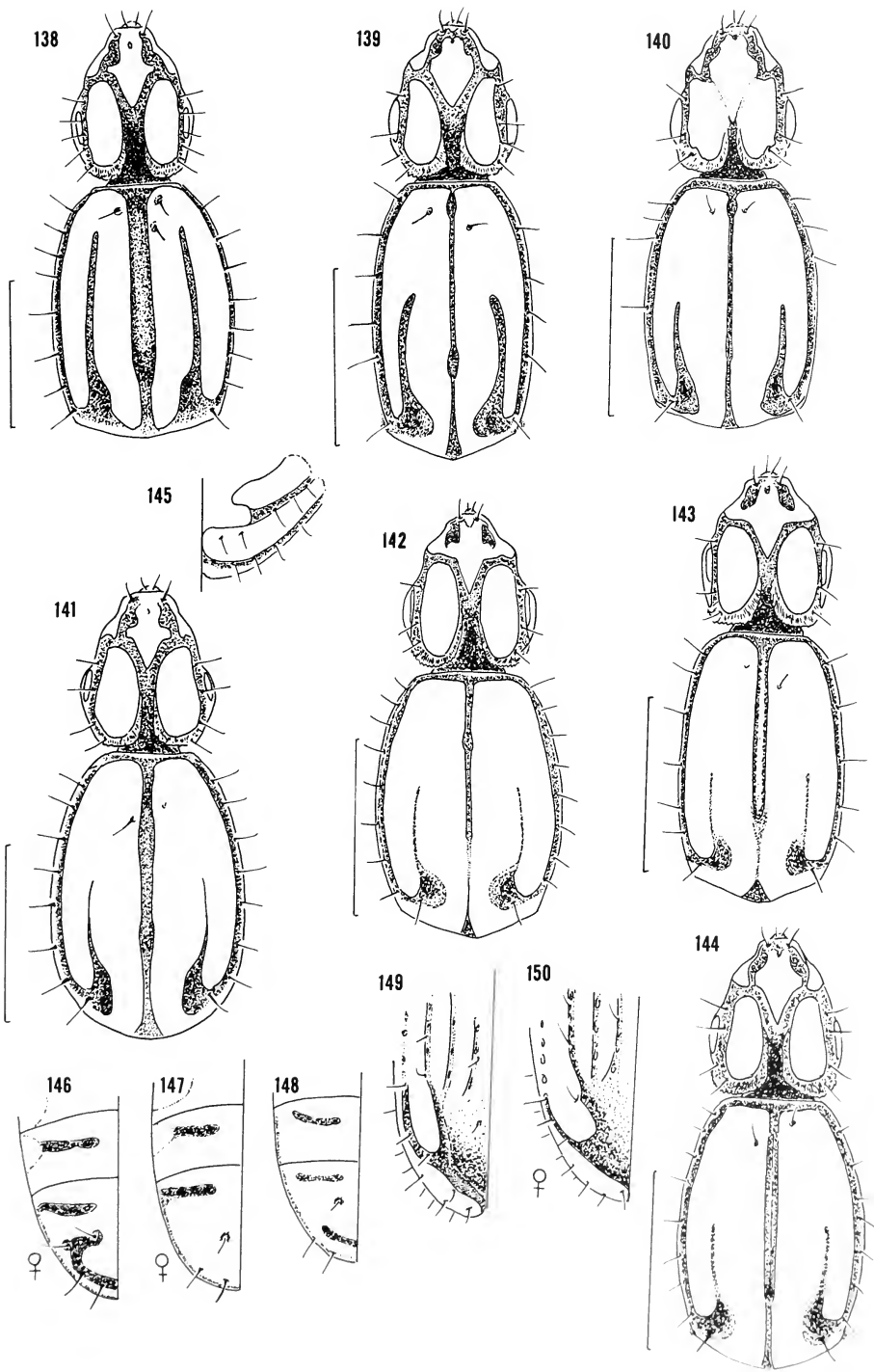


Plate 13. Figs. 151–162. Subgenus *Clinidium sensu stricto*. Figs. 151–157, Head and pronotum, dorsal aspect; Fig. 151, *C. (s. str.) trionyx* new species; Fig. 152, *C. (s. str.) haitiense* Bell; Fig. 153, *C. (s. str.) corbis* Bell; Fig. 154, *C. (s. str.) jamaicense* Arrow; Fig. 155, *C. (s. str.) chiolinoi* Bell; Fig. 156, *C. (s. str.) rossi* Bell; Fig. 157, *C. (s. str.) dormans* new species; Figs. 158–159, Elytra, posterior aspect; Fig. 158, *C. (s. str.) jamaicense* Arrow; Fig. 159, *C. (s. str.) chiolinoi* Bell; Fig. 160, Sterna V–VI, right half, male, *C. (s. str.) trionyx* new species; Fig. 161, Head, left lateral aspect, *C. (s. str.) trionyx* new species; Fig. 162, Left elytron, apex, dorsal aspect, *C. (s. str.) dormans* new species.

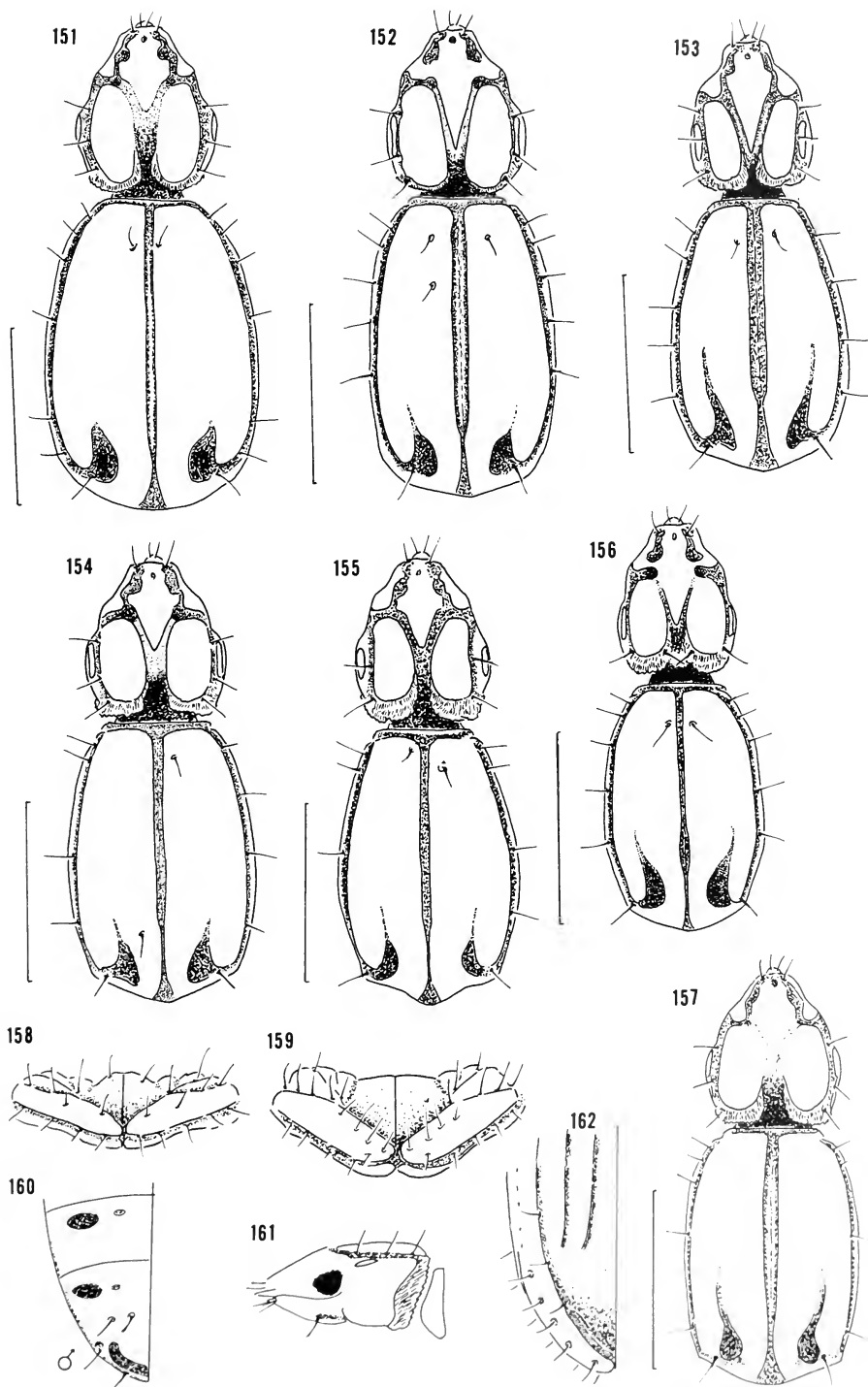


Plate 14. Figs. 163–178. Subgenus *Clinidium sensu stricto*. Figs. 163–169, Head and pronotum, dorsal aspect; Fig. 163, *C. (s. str.) penicillatum* new species; Fig. 164, *C. (s. str.) segne* new species; Fig. 165, *C. (s. str.) kochalkai* new species; Fig. 166, *C. (s. str.) planum* (Chevrolat); Fig. 167, *C. (s. str.) guildingii* Kirby; Fig. 168, *C. (s. str.) microfossatum* new species; Fig. 169, *C. (s. str.) smithsonianum* new species; Fig. 170, Hind leg (excluding tarsus), female, *C. (s. str.) penicillatum* new species; Figs. 171–173, Left elytron, apex, dorsal aspect; Fig. 171, *C. (s. str.) microfossatum* new species; Fig. 172, *C. (s. str.) planum* (Chevrolat); Fig. 173, *C. (s. str.) segne* new species; Figs. 174–175, Sternum VI, female; Fig. 174, *C. (s. str.) guildingii* Kirby; Fig. 175, *C. (s. str.) smithsonianum* new species; Fig. 176, Sternum VI, lateral aspect, female, *C. (s. str.) guildingii* Kirby; Figs. 177–178, Elytra, posterior aspect; Fig. 177, *C. (s. str.) guildingii* Kirby; Fig. 178, *C. (s. str.) smithsonianum* new species.

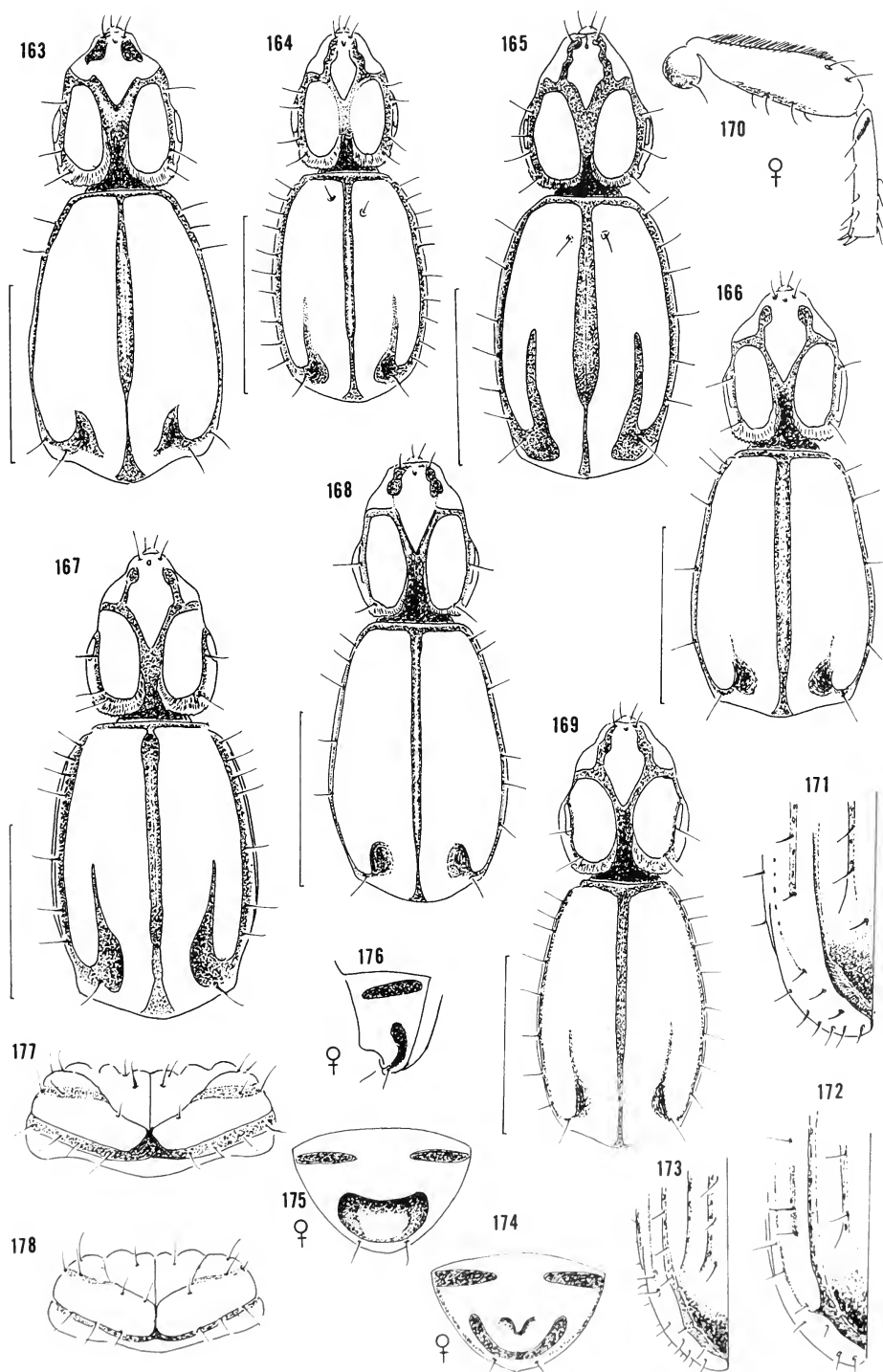


Plate 15. Figs. 179–193 Subgenus *Clinidium sensu stricto*. Figs. 179–183, Head and pronotum, dorsal aspect; Fig. 179, *C. (s. str.) rojasi* Chevrolat; Fig. 180, *C. (s. str.) bechyneorum* new species; Fig. 181, *C. (s. str.) humile* new species; Fig. 182, *C. (s. str.) mathani* Grouvelle; Fig. 183, *C. (s. str.) cavicolle* Chevrolat; Fig. 184, Anterior leg (excluding tarsus), male, *C. (s. str.) rojasi* Chevrolat; Fig. 185, Elytra, posterior aspect, *C. (s. str.) rojasi* Chevrolat; Figs. 186–191, Sternum VI; Fig. 186, *C. (s. str.) rojasi* Chevrolat; Fig. 187, *C. (s. str.) bechyneorum* new species; Fig. 188, *C. (s. str.) excavatum* new species; Fig. 189, *C. (s. str.) pala* new species; Fig. 190, *C. (s. str.) humile* new species; Fig. 191, *C. (s. str.) cavicolle* Chevrolat; Fig. 192, *C. (s. str.) mathani* Grouvelle; Fig. 193, Left elytron, dorsal aspect, *C. (s. str.) mathani* Grouvelle.

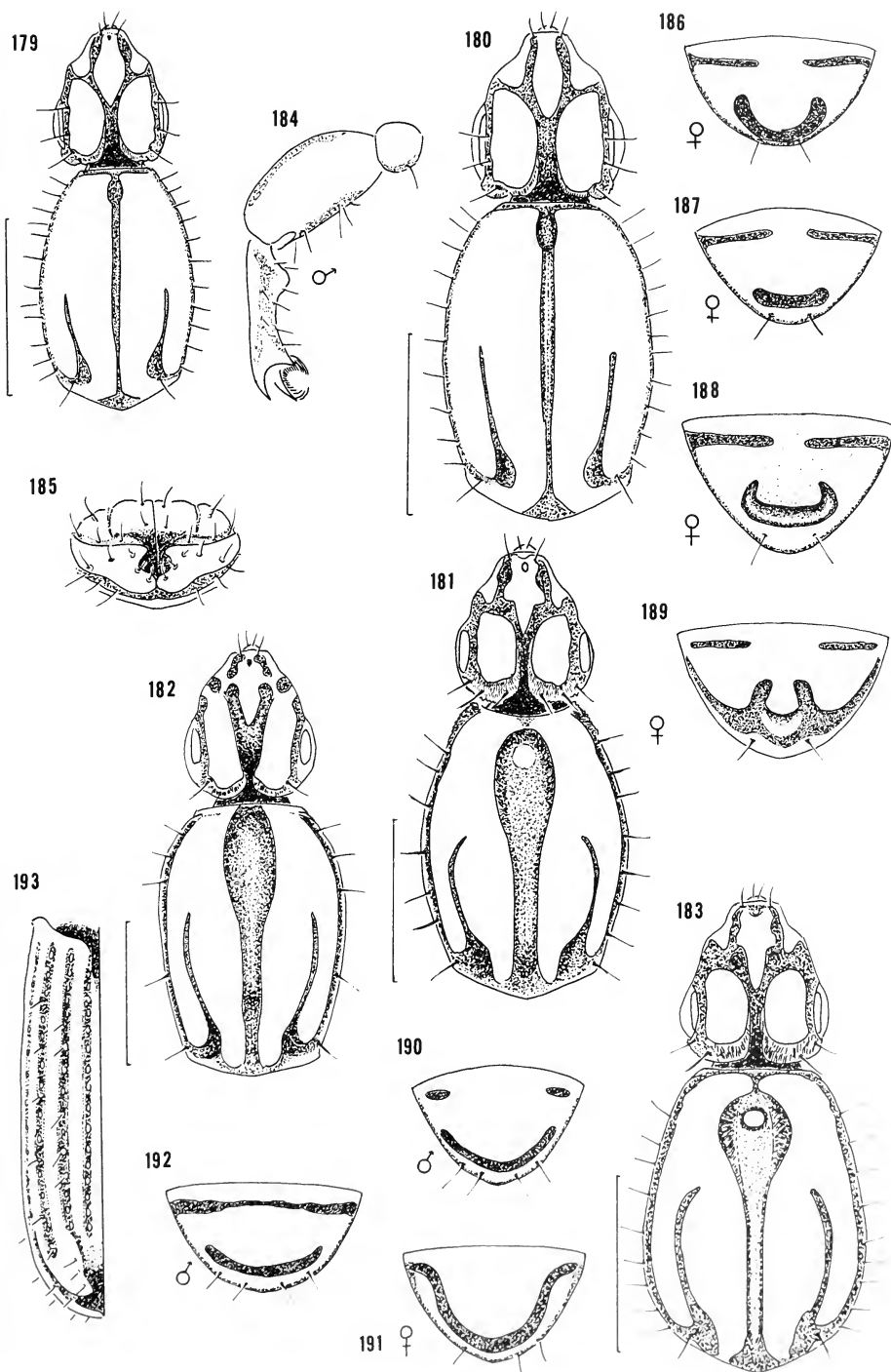
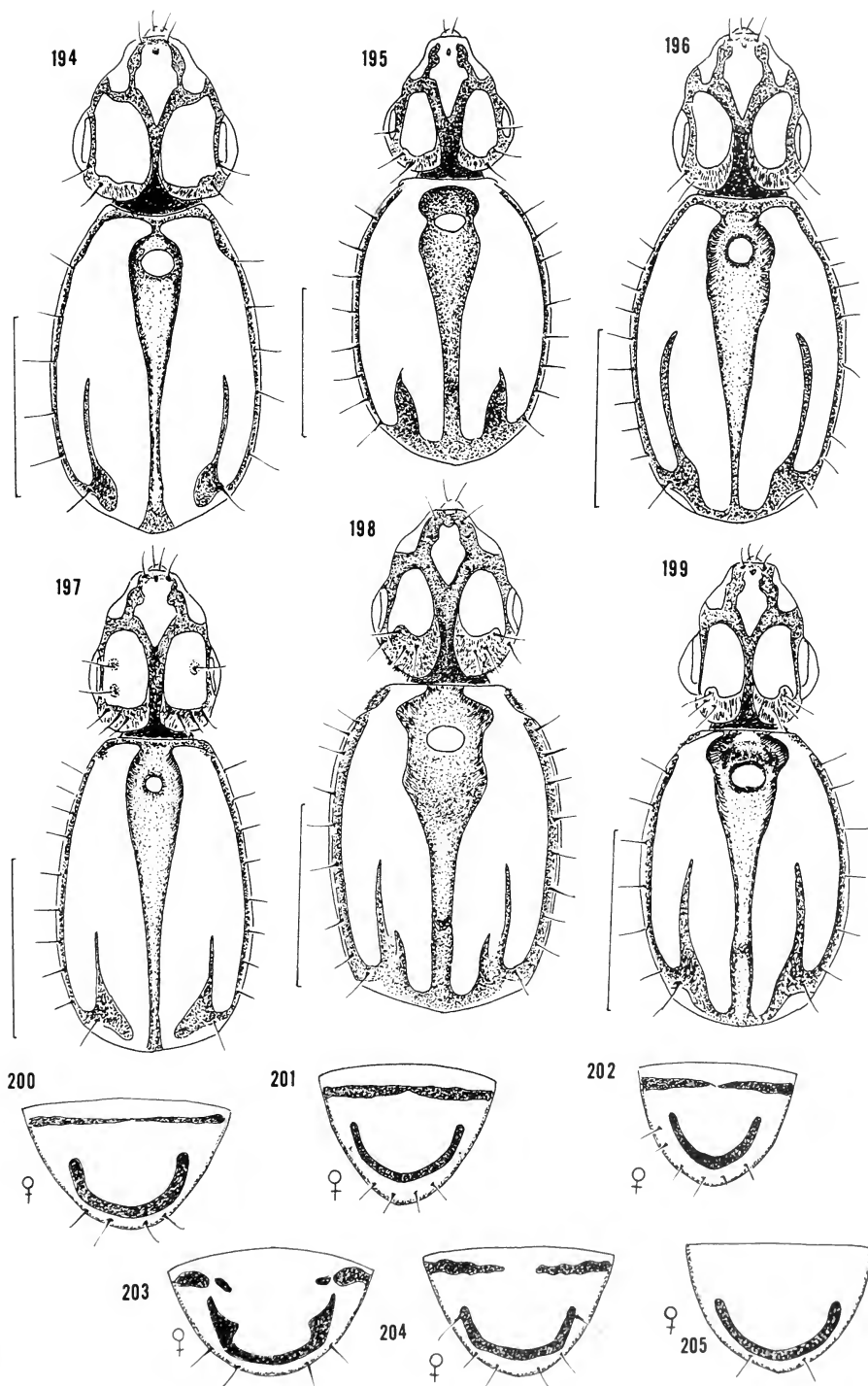


Plate 16. Figs. 194–205. Subgenus *Clinidium sensu stricto*. Figs. 194–199, Head and pronotum, dorsal aspect; Fig. 194, *C. (s. str.) curvatum* new species; Fig. 195, *C. (s. str.) foveolatum* Grouvelle; Fig. 196, *C. (s. str.) crater* new species; Fig. 197, *C. (s. str.) centrale* Grouvelle; Fig. 198, *C. (s. str.) spatulatum* new species; Fig. 199, *C. (s. str.) validum* Grouvelle; Figs. 200–205, Sternum VI, female; Fig. 200, *C. (s. str.) centrale* Grouvelle; Fig. 201, *C. (s. str.) spatulatum* new species; Fig. 202, *C. (s. str.) validum* Grouvelle; Fig. 203, *C. (s. str.) curvatum* new species; Fig. 204, *C. (s. str.) foveolatum* Grouvelle; Fig. 205, *C. (s. str.) crater* new species;



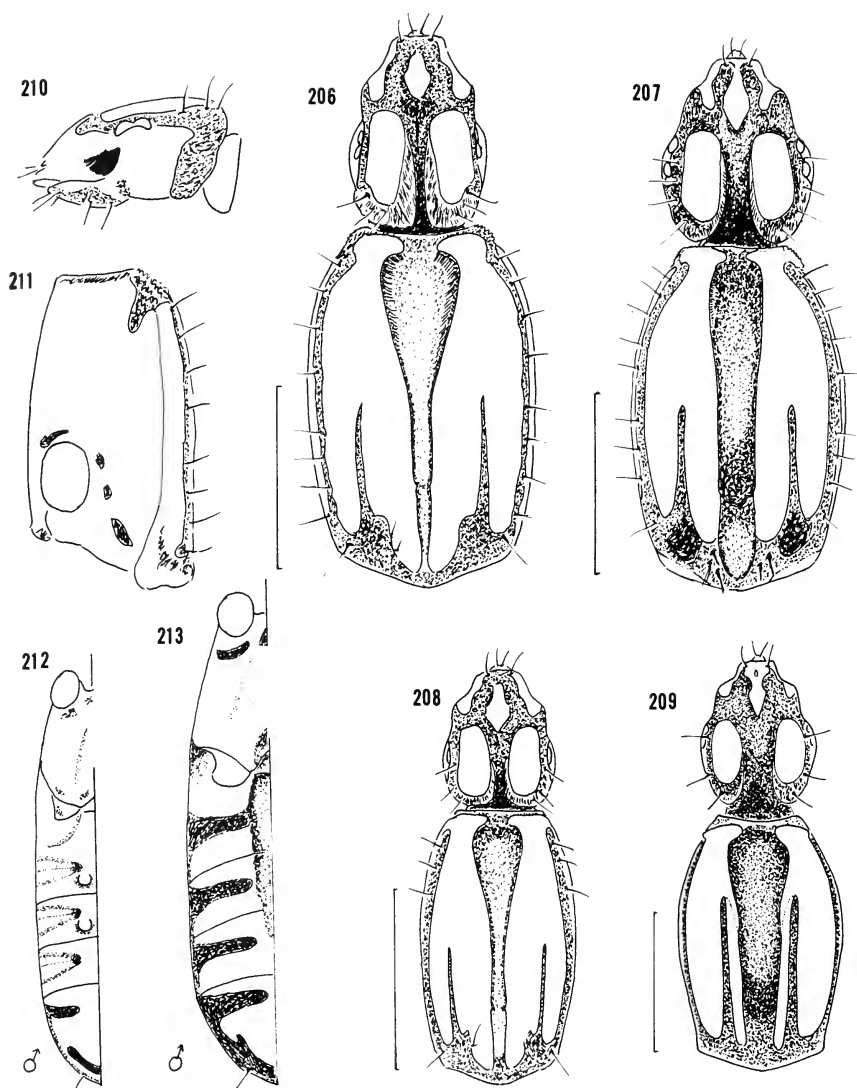


Plate 17. Figs. 206–213. Subgenus *Clinidium sensu stricto*. Figs. 206–209, Head and pronotum, dorsal aspect: Fig. 206, *C. (s. str.) moldenkei* new species; Fig. 207, *C. (s. str.) argus* new species; Fig. 208, *C. (s. str.) sulcigaster* Bell; Fig. 209, *C. (s. str.) beccarii* Grouvelle (redrawn from sketch by R. Poggi); Fig. 210, Head, left lateral aspect, *C. (s. str.) moldenkei* new species; Fig. 211, Prothorax, left lateral aspect, *C. (s. str.) moldenkei* new species; Figs. 212–213, Metasternum, abdomen, right half; Fig. 212, *C. (s. str.) moldenkei* new species, male; Fig. 213, *C. (s. str.) sulcigaster* Bell, male.

Clinidium (sensu stricto) hammondi new species

(Figs. 125, 133)

Type Material.— HOLOTYPE male, labelled: "Bogota, Rhyzophagus ?, *Clinidium granatense* Chaudoir" (BMNH). The type is in poor condition, broken into several pieces, but all important parts are present.

Description.— Length 6.0 mm. Antennal stylet very long, 0.4 as long as Segment XI; minor setal tufts present on Segments VII-X; basal setae present on Segments VIII-X, sparse on VIII; antenna devoid of pollinosity; head triangular, clearly broader than long; frontal grooves very shallow, obsolete anteriorly; median lobe short, broadly triangular, tip acute, opposite anterior part of eye; temporal lobes convergent posteriorly, forming rounded medial angles, which are narrowly separated; temporal lobe rounded posteriorly; eye short, rather broadly crescentic; orbital groove pollinose, complete, joined posteriorly to rather broad marginal band of pollinosity; one temporal seta, in prominent puncture near occipital margin; one pair of postlabial setae.

Pronotum oval, rather short, length/greatest width 1.40; widest near middle; sides strongly curved, apex truncate, base rounded; median groove deep, linear; anterior median pit enlarged, round, width about 0.20 of width of pronotum; basal impression open posteriorly, laterally, narrowed anteriorly, connecting to slightly curved discal striole, latter extending to middle of pronotum; medial part of disc sloped towards median groove; lateral part of disc convex; marginal groove prominent, visible in dorsal view; angular seta present; one marginal seta, just anterior to angular; notopleural suture glabrous; sternopleural groove nearly complete, interrupted near coxa; precoxal setae absent.

Elytra rather elongate; intervals convex; striae impressed, punctured, pollinose; sutural, parasutural striae complete, anastomosing posteriorly; intercalary intratubercular, marginal striae entire; preapical tubercle strongly inflated, rounded; apical tubercles slightly inflated, contiguous (Fig. 133); sutural, parasutural striae without setae; intercalary stria with complete row of four or five setae; one seta at apex of intratubercular stria; three or four setae in apical 0.2 of marginal stria; one seta each on apical, preapical tubercles; metasternum with complete median sulcus; transverse sulci of abdomen coarsely punctate, pollinose, those of Sterna III, IV continuous, that of V narrowly interrupted in midline in male; Sternum VI with transverse sulci joined to submarginal sulcus; Sternum VI with two setae; male without ventral tooth on anterior femur, without proximal tooth on anterior tibia; middle calcar narrow, triangular, its tip obliquely truncate; hind calcar smaller than middle one, raised above level of spurs; tibial spurs equal, large, false spur absent; female unknown.

This species is similar to *C. granatense* Chevrolat, but differs in having the intercalary stria entire and deeply impressed, and the middle calcar truncate. It is a pleasure to name this species for Peter Hammond, of the British Museum of Natural History, in gratitude for his aid in this project.

Clinidium (sensu stricto) granatense Chevrolat 1873a

(Figs. 126, 134)

Clinidium granatensis Chevrolat 1873a: 216

Clinidium granatense (Chevrolat) Grouvelle 1903 (grammatical correction).

Clinidium (sensu stricto) granatense (Chevrolat) Bell and Bell 1978.

Type Material.— LECTOTYPE (here designated) female, labelled: "Nov. Gren., *Clinidium granatense*, Chev. type" (MNH). PARALECTOTYPES one female, labelled "Nou Granada, Madellin, Typus, *granatense*" (NMW); one male, labelled: "Bogota, *granatense*, Chevrolat, Typus" (NMW).

Description.— Length 5.3-6.8 mm. Antennal Stylet very long, 0.4 as long as Segment XI; minor setal tufts present on Segments VII-X; basal setae present on Segments VII-X or VIII-X; antenna devoid of pollinosity; head triangular, clearly broader than long; frontal grooves very shallow, obsolete anteriorly; median lobe short, broadly triangular, tip acute, opposite anterior part of eye; temporal lobes convergent posteriorly, forming rounded medial angles, latter narrowly separated; temporal lobe rounded posteriorly; eye short, rather broadly crescentic; orbital groove pollinose, complete, joined posteriorly to rather broad marginal band of pollinosity; one temporal seta, in prominent puncture at margin of pollinosity near posterior margin of temporal lobe; one pair of postlabial setae.

Pronotum slightly more elongate than that of *C. hammondi*, length/greatest width about 1.48; widest near middle, sides strongly curved; apex truncate, base rounded; median groove deep, linear; anterior median pit enlarged, width about 0.20 of width of pronotum; basal impression open posteriorly, laterally, narrowed anteriorly, connecting to discal striole, latter extending to middle of pronotum; marginal groove prominent, visible in dorsal view; angular seta present; marginal setae absent; notopleural suture glabrous; sternopleural groove nearly complete, interrupted near coxa; precoxal setae absent.

Elytra rather elongate; intervals convex; striae impressed, coarsely punctured; pollinosity less continuous than in *C. hammondi*; sutural, parasutural striae complete, anastomosing near apex; intercalary stria abbreviated, ending blindly at anterior part of preapical tubercle; intratubercular, marginal striae entire; preapical tubercle inflated, rounded; apical

tubercles inflated, contiguous (Fig. 134); sutural, parasutural striae without setae; intercalary stria with complete row of four or five setae; one or two setae at apex of intratubercular stria; four or five setae in apical 0.2 of marginal stria; one seta each on apical, preapical tubercles; metasternum with complete median sulcus; transverse sulci of abdominal sterna coarsely punctate, pollinose, continuous on Sternum III in both sexes, continuous on IV in male, narrowly interrupted in female; widely separated on V in both sexes, Sternum VI with transverse sulci joined to submarginals; Sternum VI with two setae; lateral pits present on both III, IV in both sexes very small in male; female with small median pit on Sternum VI; male without ventral tooth on anterior femur, without proximal tooth on anterior tibia; middle calcar triangular, acute; hind calcar broadly triangular, tip acute, raised above level of spurs; tibial spurs large, equal, false spur absent.

The abbreviated intercalary stria and the different shape of the middle calcar separate this species from *C. hammondi*, to which it is otherwise strongly similar.

Clinidium (sensu stricto) incudis Bell 1970

(Figs. 127, 132)

Clinidium (sensu stricto) incis Bell 1970: 319.

The original spelling, *incis*, is incorrect. The name is derived from *incus* (anvil), based on the type locality, El Yunque, the Spanish word for anvil. The genitive singular form of the word is *incudis* ("of the anvil").

Type Material.— HOLOTYPE male, labelled: "El Yunque, Puerto Rico, May, 1938, coll. P. J. Darlington" (MCZ 31756). PARATYPES two females with same data as type (MCZ); two males, two females, from the same locality, coll. T. B. Hlavac, L. Herman, Jr., 2200-3200 ft., Feb. 15-24, 1969 (MCZ).

Description.— Length 6.1-7.5 mm. Antennal stylet very long, about 0.5 as long as Segment XI; tufts of minor setae present on Segments VII-X; basal setae entirely absent; Segments I-V each with subapical pollinose ring; head longer than broad; frontal grooves linear, nearly glabrous, deeper than in preceding species; median lobe triangular, tip acute, posterior to eye; temporal lobes divergent posteriorly, not forming medial angles; temporal lobe rounded posteriorly, broadly bordered with pilosity; eye minute, round, protruding, resembling an ocellus, located near middle of length of head; orbital groove deeply impressed, pollinose, complete; two temporal setae; one pair of postlabial setae.

Pronotum rather short, length/greatest width 1.40; widest anterior to middle, lateral margins curved anteriorly, oblique posteriorly; margin shallowly sinuate anterior to hind angle; median groove deep, rather broad, parallel posteriorly, anteriorly gradually broadened to anterior median pit; latter large, about 0.25 of width of pronotum at level of pit; basal impression small, triangular, closed posteriorly; discal striole curved, extending to middle of pronotum; marginal groove linear, visible in dorsal view; angular seta present; two marginal setae, anterior to middle of pronotum; two pairs of discals, opposite anterior part of anterior median pit; one pair of basals, medial to basal impressions; notopleural suture glabrous; anterior part of sternopleural suture very shallow, incomplete; precoxal setae absent.

Elytra rather elongate; intervals convex; striae impressed, pollinose, inconspicuously punctate; all striae, including intercalary, complete; preapical tubercle strongly inflated; apical tubercles inflated, nearly contiguous, but separately rounded; sutural stria without setae; parasutural stria with two or three setae, anterior one near or anterior to middle; intercalary stria with complete row of four or five setae; one seta near apex of intratubercular stria; marginal stria with two to six setae in posterior 0.5; preapical tubercle with one seta; apical tubercle with one to three setae; metasternum without median sulcus; abdominal Sterna III-VI each with uninterrupted transverse sulcus, latter consisting of row of very coarse punctures; that of Sternum VI not joined to submarginal groove; Sternum VI of female with median pit; female with deep lateral pit on Sternum IV; male without ventral tooth on anterior femur, but with small triangular proximal tooth on anterior tibia; calcars triangular, dorsal margin separated from tibia by deep notch; tibial spurs large, equal; false spur absent.

The form of the eye is unique within the genus though it recalls those of *Shyrodes dohertyi* (Grouvelle) and *Srimara planicollis* Bell and Bell. This is the only species from the West Indies which has the anterior median pit enlarged. The eye, the anterior median pit, and the divergent temporal lobes easily separate this species from the only other Rhysodine from Puerto Rico, *Clinidium (sensu stricto) boroquense* Bell.

Range.— Puerto Rico. We have seen additional specimens from El Yunque, and have collected it there ourselves. In addition, we have seen a specimen labelled "Puerto Rico: Villalba, C. M. Matos, VI-30-1938" (MAY).

Bionomics.— Host species have not been recorded. Bell (1970) quotes observations by Hlavac (in litt.) on this species in the field and its behavior in the laboratory.

THE *INSIGNE* GROUP

In this group, the tufts of minor setae are present on Segments VI-X. The eye is crescentic. The form of the anterior median pit varies among the species. This group contains four species, two from northwestern South America, one from the "continental" island of Trinidad, and one from Puerto Rico.

Phylogeny.— The Ecuadorian species, *C. dubium*, is very different from the remaining ones, and possibly had an independent origin from the *cavicolle* group, which it resembles except in the absence of the tuft of setae from antennal Segment V. The rest of the species share the following characters: temporal lobes convergent posteriorly; antennal stylet rather small; anterior tibia of male without proximal tooth; anterior median pit medium to small, without tubercle. *C. boroquense* stands apart from the remaining two, in having the intercalary stria complete, the metasternum not sulcate, and the intratubercular stria not impressed except at the apex. The Ecuadorian (and possibly Colombian) species, *C. insigne*, is obviously closely related to *C. howdenorum* of Trinidad, despite the wide geographic separation of the two.

Clinidium (sensu stricto) dubium Grouvelle 1903
(Fig. 128)

Clinidium dubium Grouvelle 1903: 129-130.

Clinidium (sensu stricto) dubium (Grouvelle) Bell and Bell 1978.

Type Material.— HOLOTYPE male, labelled: "Loja, Ecuador, *C. dubium* type" (MNHN).

Description.— Length 5.7 mm. Antennal stylet very long, 0.4 as long as Segment XI, acuminate; tufts of minor setae present on Segments VI-X; basal setae present on Segments VI-X, sparse on VI; Segments I-VII with subapical pollinose bands; head with length, width approximately equal; frontal grooves rather fine, shallow; median lobe triangular, tip acute, opposite middle of eye; temporal lobe divergent posteriorly, posterior margin rounded; bordered with pilosity; eye small, narrowly crescentic, about 0.25 of length of temporal lobe; orbital groove complete, pollinose; one or two temporal setae; two pairs of postlabial setae.

Pronotum rather short, length/greatest width 1.36; widest slightly anterior to middle, lateral margins curved, becoming oblique posteriorly; median groove deep, rather broad, slightly constricted near middle, anteriorly broadened gradually, slightly sinuate where joined to anterior median pit; latter large, about 0.25 of width of pronotum at level of pit; anterior median pit with round pollinose central tubercle; basal impression elongate, triangular, closed posteriorly, about 0.25 as long as pronotum; discal striole not distinct; marginal groove visible in dorsal view; three or four marginal setae; angular seta absent; notopleural suture glabrous; sternopleural groove complete, pollinose; precoxal setae absent.

Elytra moderately elongate; striae impressed, pollinose, inconspicuously punctate; intercalary stria abbreviated posteriorly, ending blindly at level of anterior end of preapical tubercle; other striae entire; preapical tubercle inflated; apical tubercles inflated, contiguous; intercalary stria with complete row of three or four setae; intratubercular stria with one seta near apex; marginal stria with six or seven setae in apical 0.2; metasternum with complete, deep median sulcus; hind coxa with conspicuous pollinose area on lateral margin; male with complete transverse sulci on Segments II-VI; submarginal groove of Sternum VI not connected to transverse sulcus; male without ventral tooth on anterior femur, but with acute proximal tooth on anterior tibia; calcars narrow, acute; tibial spurs equal, false spur absent.

This is the only species in the group that has a large anterior median pit with a central tubercle. It is similar to members of the *cavicolle* group except in lacking a tuft on Segment V. It will not key to any member of the *cavicolle* group, since the only member of the latter group, *C. mathani*, to have the intercalary stria abbreviated posteriorly, lacks a central tubercle in the anterior median pit and has long discal strioles on the pronotum.

Clinidium (sensu stricto) insigne Grouvelle 1903
(Figs. 131, 135, 136)

Clinidium insigne Grouvelle 1903: 132.

Clinidium (sensu stricto) insigne (Grouvelle) Bell and Bell 1978.

Type Material.— According to the original description, the type was from Ecuador, and was in the Oberthür collection. We were unable to locate a specimen labelled as a type. Possibly the description was based on a female specimen, labelled: "Ecuador, Slemiradski 1882-1883, *Clinidium insigne* Grouv." (MNHN), though this was not labelled as a type, it is the only specimen of this species among the material studied by Grouvelle.

Description.— Length 7.0-7.4 mm. Antennal stylet conical, acuminate, moderately long, about 0.25 of length of Segment XI; tufts of minor setae present on Segments VI-X; basal setae present on Segments VII-X; Segment I with pollinose subapical band; pollinosity otherwise absent from antenna; head with length, width almost equal; frontal grooves narrow, deep, pollinose; median lobe triangular, narrow, tip acute, just behind level of anterior margin of eye; temporal lobes strongly convergent posteriorly, forming lobate medial angles, latter very narrowly separated; posterior margin rounded, bordered with pollinosity; eye crescentic about 0.5 length of temporal lobe; orbital groove complete, pollinose; one temporal seta arising from large pollinose puncture touching posteriolateral pollinose border of temporal lobe; two pairs of postlabial setae.

Pronotum long, length/greatest width 1.60; widest near middle, sides curved; base rounded; median groove deep, narrow, sides parallel except at slight expansion at basal 0.33 of length; anterior median pit elongate, oval, about 0.15 of width of pronotum opposite the pit; central tubercle absent; basal impression narrow, oblong, open posteriorly; discal striole deep, nearly straight, extending anteriorly beyond middle of pronotum; marginal groove deep, visible in dorsal view; six marginal setae, angular seta absent; notopleural suture glabrous; sternopleural groove nearly complete, narrowly interrupted near coxa; precoxal setae absent.

Elytra moderately elongate; striae impressed, pollinose, inconspicuously punctate; intercalary stria abbreviated posteriorly, ending blindly at level of anterior end of preapical tubercle; other striae entire; preapical tubercle strongly inflated, truncate posteriorly; apical tubercles strongly inflated, rounded, contiguous; parasutural striae without setae; intercalary stria with complete row of three to five setae; intratubercular stria with one or two setae near apex; marginal stria with six or seven setae in apical 0.33; preapical tubercle with one seta; apical tubercle with one seta; metasternum with deep, complete median sulcus; female with transverse sulci complete on Sterna III-IV, interrupted on midline on V, VI; female with transverse sulci of Sternum VI joined to submarginal groove; Sternum VI with two setae; female with large lateral pit on Sternum IV (Fig. 135); tibial spurs slightly unequal; false spur absent.

We provisionally assign a male, labelled: "Cali, Cauca, Colombia, VI-30-38, C. H. Seevers" (CNHM) to this species. It differs from the female holotype in having the transverse sulcus of Sternum V continuous and the submarginal groove of Sternum VI widely separated from the transverse sulci (Fig. 136). The first of these characters is likely to be a secondary sexual difference, but the second is not. It might be a separate, but closely allied species. The male from Cali has the following secondary sexual characters: anterior femur without ventral tooth; anterior tibia without proximal tooth; both calcars angulate dorsally; middle calcar longer than hind one; tips of calcars obtuse.

This species is closest to *C. howdenorum* of Trinidad, which has a narrower head, more elytral setae, and a differently shaped preapical lobe on the elytra.

Clinidium (sensu stricto) howdenorum new species
(Fig. 130)

Type Material.— HOLOTYPE male, labelled: "Morne Blue, 2700' TRINIDAD, W.I., Aug. 19, 1969, H. & A. Howden" (BSRI).

Description.— Length 6.0 mm. Antennal stylet flattened, narrowly, obliquely truncate, 0.2 of length of Segment XI; tufts of minor setae present on Segments VI-XI; basal setae present on Segments VI-X; Segment I with pollinose subapical band; pollinosity otherwise absent from antennae; head longer than wide; narrower, more convex than in *C. insigne*; frontal grooves narrow, deep, pollinose; median lobe very narrow, tip acute, posterior to level of anterior margin of eye; temporal lobes strongly convergent posteriorly, forming lobate medial angles, latter very narrowly separated; posterior margin rounded; eye crescentic about 0.15 of length of temporal lobe; orbital groove complete, pollinose; three temporal setae, respectively anterior to, opposite, posterior to eye; each seta base surrounded by pollinosity, latter extensively "scalloping" lateral margin of temporal lobe; orbital groove complete; three pairs of postlabial setae.

Pronotum elongate, but less so than in *C. insigne*; length/greatest width 1.50; widest near middle, sides curved; base rounded; median groove deep, narrow, sides parallel except at slight expansion at basal 0.33 of length; anterior median pit elongate, oval, about 0.20 of width of pronotum at pit; central tubercle absent; basal impression triangular, open posteriorly; discal striole deep, curved, extending anteriorly beyond middle of pronotum; marginal groove deep, visible in dorsal view; angular seta present; eight marginal setae; notopleural suture glabrous; sternopleural groove nearly complete, narrowly interrupted opposite coxa; precoxal setae absent.

Elytra moderately elongate; striae impressed, pollinose, inconspicuously punctate; intercalary stria abbreviated posteriorly, ending blindly at level of anterior end of preapical tubercle; remaining striae entire; preapical tubercle strongly inflated, medial angles lobate; medial margin of tubercle emarginate opposite tip of intercalary stria (Fig. 137); apical tubercles inflated, rounded, contiguous; parasutural stria with 10 setae; intercalary with nine setae; intratubercular stria with three or four setae near apex; marginal stria with 10-12 setae; preapical tubercle with three setae; apical tubercle with one seta; metasternum with deep, complete median sulcus; male with transverse sulcus narrowly interrupted on Sternum III, V, VI, complete on Sternum IV; male with distinct lateral pit on Sternum IV; Sternum VI with submarginal sulcus broadly separated from transverse sulcus; Sternum VI with four setae; tibial spurs equal; false spur absent; male without ventral tooth on anterior femur, without proximal tooth on anterior tibia; middle calcar acute, smaller than hind calcar; latter narrowly truncate.

This species is obviously closest to *C. insigne*, but differs in the form of the antennal stylet, in the head being narrower and more convex, the elytral setae being much more numerous, and in the preapical tubercles being lobate.

It is a pleasure to name this species, the first described from Trinidad, after the collectors, Anne and Henry Howden.

Clinidium (sensu stricto) boroquense Bell 1970
(Figs. 129, 137)

Clinidium (sensu stricto) boroquense Bell 1970:321.

Type Material.— HOLOTYPE male, labelled: "El Yunque, Puerto Rico, May, 1938, coll. P. J. Darlington" (MCZ 31757). PARATYPES, one male, one female, same label as holotype (MCZ); one male, from same locality, coll. T. B. Hlavac, L. Herman, Jr., 2200-3200 ft., Feb. 15-24, 1969 (MCZ).

Description.— Length 4.0-5.9 mm. Antennal stylet minute; tufts of minor setae present on Segments VI-X; basal setae present, but sparse on Segments IX-X; Segment I with pollinose subapical band; pollinosity otherwise absent from antenna; head slightly longer than wide; frontal grooves fine, scarcely pollinose; median lobe triangular, short, tip opposite anterior 0.2 of eye; temporal lobes convergent posteriorly, forming rounded, nearly contiguous medial angles; frontal space very narrow, posterior margin of temporal lobe rounded, very narrowly margined with pilosity; lateral margin of head only slightly curved; eye very narrowly crescentic, about 0.8 of length of temporal lobe; orbital groove complete, pollinose but very narrow; two or three temporal setae, one anterior to eye, one opposite middle of eye; posterior one near posterior margin of temporal lobe; two pairs of postlabial setae.

Pronotum rather long, length/greatest width 1.55; widest near middle, sides curved, abruptly rounded, narrowed to apex, more gradually rounded to base; latter curved; margin shallowly sinuate anterior to hind angle; median groove deep, nearly linear, margins parallel; anterior median pit very small, margins of median groove not at all expanded opposite it; basal impression small, triangular, closed posteriorly; discal striole fine, slightly curved, extending to middle of pronotum; marginal groove fine, visible in dorsal view; angular seta present; one or two marginals or absent, location differing among the specimens; notopleural suture glabrous; sternopleural groove absent; precoxal setae absent.

Elytra moderately elongate; striae impressed, pollinosity scant; striae punctate; all striae complete; intratubercular stria shallower than the others; preapical tubercle slightly inflated, apex of intratubercular stria shallowly impressed, so preapical, apical tubercles not strongly separated; apical tubercles inflated, rounded, slightly separated; sutural striae with one to four setae near base; intercalary stria with complete row of four or five setae; intratubercular stria with one to three setae near apex; marginal stria with three to five setae in apical 0.20; preapical tubercle without setae; apical tubercle with one seta; metasternum without median sulcus; transverse sulci of abdominal sterna impressed laterally, medial portion replaced by row of several very coarse punctures; Sternum VI on each side with two punctures in place of transverse sulcus; submarginal sulcus short; Sternum VI with two setae; female with lateral pits on Sterna IV, V; male without ventral tooth on anterior femur, without proximal tooth on anterior tibia; calcars small, triangular, acute; hind calcar raised above level of spurs; tibial spurs large, equal; false spur absent.

This species shows many points of similarity to *C. insigne* and *C. howdenorum*, especially in the distribution of tufts of minor setae and in having convergent temporal lobes. The latter species, however, has the anterior median pit enlarged, and lacks discal setae on the pronotum. *C. boroquense* is not likely to be confused with the other known Puerto Rican species, *C. incudis*, as the latter has a strongly enlarged anterior median pit, divergent temporal lobes, and an ocelliform eye.

Range.— Puerto Rico. We have seen four additional specimens from the type locality, labelled: "El Yunque, Puerto Rico, Luquillo Exp. For., Rte. 915, 1.5 mi. off Rte. 988, Mar. 29, 1976, A. Gillogly, H. Harlan" (UVM). We have seen specimens from four additional localities: "Utuaedo, 11-15-1935, A. Ramirez" (MAY);

"Adjuntas, VIII-1933, R. G. Oakley" (MAY); "5 mi. s. of Utuado, 3 July, 1979, coll. M. A. Ivie" (MAI); "Aguas Buenas, forest at Aguas Buenas cave, 7-17-V-73, 250 m., S. Peck et al" (BSRI).

THE *GUILDINGII* GROUP

In this group, the tufts of minor setae are found on Segments V-X of the antenna, and the anterior median pit is very small. In most species, the median groove is not widened at the anterior median pit, while in a few species it is slightly widened. Most species have false spurs on the middle and hind tibiae. A false spur is a rigid tooth projecting from the apical margin of the tibia. In size and shape it resembles the true spurs. The eyes are narrow and crescentic. Some species have a broad tooth or a slight cusp in place of the false spur.

This group is the largest in the subgenus, with 25 species. The range is substantially that of the subgenus, except that members of this group are not known at present from Puerto Rico, French Guiana, or Guatemala.

Phylogeny.— We provisionally divided the group into five sections. The *oberthueri* section has both intercalary and intratubercular striae complete, and has the metasternum sulcate, sometimes only very shallowly so. The *jamaicense* section has similar striation, but lacks the metasternal sulcus. The *rossi* section has the intercalary stria complete, but has the intratubercular not impressed near the apex, so that the preapical and apical tubercles are fused. The metasternal sulcus is absent in *C. rossi*, but present in the other members of the section. The *guildingii* section has the intercalary stria abbreviated posteriorly, and the metasternum not sulcate. The *rojasi* section has the intercalary stria abbreviated and the metasternum sulcate.

The interrelationships among these sections can be analyzed in various ways, depending on which character states are regarded as derived. We regard the features of the *oberthueri* section as being primitive within the subgenus. Although the absence of a metasternal sulcus is probably a primitive character in the Rhysodini as a whole, it appears to us that a sulcus was present in the common ancestor of *Clinidium sensu stricto*, and has been secondarily lost three times in the *guildingii* group, in *C. rossi*, and in the ancestors of the *jamaicense* and *guildingii* sections. All but *C. rossi* are West Indian species. The metasternal sulcus is also absent in West Indian species of the *insigne* and *granatense* groups. This seems to be an unusual example of convergent evolution, comparable to the strongly narrowed outer pronotal carinae in members of various genera and subgenera of Omoglymmiina from the Andaman Islands. An alternative theory would be that the presence of a median metasternal sulcus is a derived character, which arose independently in several lines in the Andean Region.

THE *OBERTHUEI* SECTION

This section contains species with the intercalary and intratubercular striae entire and the metasternum with a median sulcus. There are seven species, probably occupying two disjunct areas. Two species are found in Panama. Four others are on the eastern side of the Andes, in Ecuador, Colombia, Venezuela, and the western part of Amazonas State, Brazil. They approach the sea only in Merida State, Venezuela, south of Lake Maracaibo. The locality of *C. humboldti* is ambiguous, as Nueva Granada included both Colombia and Panama.

Phylogeny.— The two Panamanian species, *C. alleni* and *C. whiteheadi*, have the basal impression round, and sharply separated from the discal striole, which is linear. They contrast strongly with the South American species, and perhaps are not closely related to them. The

latter species have the basal impression small, triangular, and poorly separated from the dilated discal striole.

C. humboldti is closest to the two Panamanian species, but differs from both in having the antennal lobes separated from the median lobe. The common ancestor of the Panamanian species was probably the sister species of *C. humboldti*.

The four South American species can be grouped into two pairs. *C. integrum* and *C. pilosum* have the paramedian groove more than 0.5 the length of the pronotum and the frontal groove relatively broad and deep, while in *C. oberthueri* and *C. jolyi* the paramedian groove is less than 0.5 the length of the pronotum and the frontal grooves are relatively shallow and narrow.

Clinidium (sensu stricto) integrum Grouvelle 1903
(Figs. 138, 145)

Clinidium integrum Grouvelle 1903: 127-128.

Clinidium (sensu stricto) integrum (Grouvelle) Bell and Bell 1978.

Type Material.— HOLOTYPE female, labelled: "St. Paulo d'Olivencia, M. de Mathan, Mai, 1883" (MNHN). The type locality is on the Amazon River in western Amazonas State, Brazil, about 100 kilometers east of the Colombian border.

Description.— Length 6.8 mm. Antennal stylet moderately long, about 0.25 of length of Segment XI; minor setal tufts on Segments V-X; basal setae present though sparse on Segments VII-X; Segments I-X each with subapical pollinose band; head distinctly longer than wide; frontal grooves deep, rather wide; median lobe short, triangular, tip opposite anterior margin of eye; medial margins of temporal lobes curved, closest together near middle of head, divergent posteriorly; posterior margin rounded, with wide pilose border; eye narrowly crescentic, very short, about 0.33 of length of temporal lobe; head margins oblique behind eyes; orbital groove complete, pollinose; five or six temporal setae in orbital groove; two pairs of postlabial setae.

Pronotum rather short, length/greatest width 1.44; widest near middle, base only slightly narrowed, apex more strongly narrowed; lateral margins only slightly curved; apex truncate; base curved; median groove dilated, widest posterior to middle, where 0.09 of width of pronotum, slightly narrowed near apex, more suddenly narrowed near base; median groove not at all dilated at anterior median pit; basal impression narrow, open posteriorly, only moderately wider than discal striole, latter extended anteriorly 0.9 of length of pronotum; marginal groove visible in dorsal view; angular seta present; seven to 10 marginal setae; one or two discal setae; sternopleural groove absent; precoxal setae absent.

Elytra elongate; striae impressed, pollinose; all striae entire; apex of intratubercular stria deep; preapical tubercle inflated, apex angular in posterior view, overhanging preapical impression; apical tubercles inflated, rounded, contiguous; sutural stria with complete row of five or six setae; preapical impression with three setae aligned with those of sutural stria; parasutural stria with one or two setae near apex; intercalary stria with complete row of eight or nine setae; intratubercular stria with three or four setae near apex; marginal stria with complete row of about 10 setae; metasternum with deep median sulcus; abdominal sterna with transverse sulci widely interrupted in midline; female with deep lateral pit on Sternum IV; Sternum VI with eight setae; false spurs absent; male unknown.

This species is easily recognized by the great length of the discal striole of the pronotum. Within the section, the angulate preapical tubercle is also distinctive (Fig. 145).

Vulcano and Pereira (1957b) figured and described a species under this name. They did not study the type of *C. integrum*. Judging by their figure, they studied a quite different species, perhaps referable to *Rhyzodiastes*, subgenus *Rhyzotrix*.

Clinidium (sensu stricto) pilosum Grouvelle 1903
(Figs. 139, 146)

Clinidium pilosum Grouvelle 1903: 126-127.

Clinidium (sensu stricto) pilosum (Grouvelle) Bell and Bell 1978.

Type Material.— HOLOTYPE female, labelled: "Venezuela, Dr. Moritz, 1858, *Clinidium pilosum* ty. Grouvelle" (NMW). There was no red "typus" label on the specimen, but the specimen was labelled in Grouvelle's hand, and the locality and collector agree with those cited in the original description.

Description.— Length 5.6–6.0 mm. Antennal stylet moderately long, about 0.20 of length of Segment XI; minor setal tufts on Segments V–X; basal setae present on Segments IX–X; Segments I–VIII with subapical pollinose bands; head distinctly longer than wide; frontal grooves deep, rather wide; median lobe short, triangular, tip opposite anterior margin of eye; medial margins of temporal lobes nearly straight, subparallel; posterior margin rounded, with wide pilose border; eye narrowly crescentic, longer than in *C. integrum*, over 0.5 of length of temporal lobe; orbital groove complete, pollinose; four or five temporal setae in orbital groove; two pairs of postlabial setae.

Pronotum longer than in *C. integrum*; length/greatest width 1.65; widest near middle, sides nearly parallel, only slightly curved; apex *truncate*; base curved; median groove narrow, margins nearly parallel except for dilation opposite middle of discal striole and another at base; median groove not at all dilated opposite anterior median pit; basal impression narrow, closed posteriorly but open laterally, only slightly wider than discal striole; latter extended anteriorly about 0.66 of length of pronotum; marginal groove visible in dorsal view; angular seta present; six to 10 marginal setae; one or two discs on either side anteriorly, one or two on each side in basal 0.25 of length or absent; sternopleural groove absent; precoxal setae absent.

Elytra elongate, striae impressed, pollinose, coarsely punctate; all striae entire; apex of intratubercular stria rather shallow; preapical tubercle inflated, rounded; apical tubercles inflated, contiguous; sutural stria with complete row of five setae, apical impression with two aligned with those of sutural stria; parasutural stria with one seta near base; intercalary stria with complete row of nine or 10 setae; intratubercular stria with four setae near apex; marginal stria with about 18 setae in complete row; apical tubercle with about six setae; metasternum with shallow median sulcus; transverse sulci of abdominal Sternum III not interrupted in midline; that of Sternum IV not interrupted in female, interrupted in female; those of Sterna V–VI broadly interrupted; Sternum VI with submarginal groove bent inward at base, not connected to transverse sulci (Fig. 146); Sternum VI with six to eight setae, two to four in transverse row between anterior ends of submarginal sulcus, four in curving row along submarginal sulcus; female with lateral pit in Sternum IV; tibiae with false spurs present, though small; male without ventral tooth on anterior femur, nor proximal tooth on anterior tibia; calcar triangular; middle one narrow, longer, more pointed than hind one; latter with dorsal margin slightly angulate.

The very long, nearly parallel-sided pronotum is distinctive. *C. jolyi* differs in having a shorter pronotum, with the paramedian grooves less than 0.5 the length of the pronotum. Also, the parasutural stria has a complete row of setae, the submarginal groove of the sixth sternite is absent and the frontal grooves much shallower. *C. oberthueri* differs in having a much more oval pronotum, strongly narrowed at both base and apex. The eye is shorter, the frontal grooves are shallower, and precoxal setae are present.

Range.— Merida State, in western Venezuela, and possibly in adjacent parts of Colombia. In addition to the holotype, we have seen one male and two females, labelled: “Venezuela, Merida, La Azulita, 2000 m., 5.6-X-69, J. and B. Bechyne leg.” (VEN), and a male, with a handwritten label which is difficult to interpret, but which appears to us to read “Cae Lun, N., Columb., Mor. 8129” (MNHB).

Clinidium (sensu stricto) jolyi new species (Figs. 140, 147)

Type Material.— HOLOTYPE male, labelled: “VENEZUELA, Mérida, La Azulita, 2000 m., 6-X-69, J. & B. Bechyne, leg.” (VEN). PARATYPES two males, labelled: “Venezuela, Merida, La Mucuy, 30-VIII-1956, C. J. Rosales col.” (VEN); one male, one female, labelled: “Venezuela, Merida, Carbonera, 2600 m, 3-X-69, J. & B. Bechyne” (VEN).

Description.— Length 5.0–6.0 mm. Antennal stylet rather small, about 0.16 of length of Segment XI; minor setal tufts on Segments V–X; basal setae present on Segments IX, X; Segments I–IV with subapical pollinose bands; head slightly longer than wide; frontal grooves very shallow, linear, glabrous; median lobe short, triangular, ending just posterior to anterior margin of eye; medial margins of temporal lobes slightly divergent posteriorly; posterior margin transverse; posterior margin with very broad pilose border, this extending anteriorly along medial margin; eye narrowly crescentic, shorter than in *C. pilosum*, about 0.4 of length of temporal lobe; orbital groove complete, pollinose; three temporal setae, two opposite eye, the other behind eye, distant from margin, its base included in dilation of marginal pilose band; two postlabial setae.

Pronotum shorter than in *C. pilosum*; length/greatest width about 1.48; widest near middle, sides curved; base, apex nearly equally narrowed; apex *truncate*; base curved; median groove narrow, margins nearly parallel; groove scarcely dilated opposite anteriomedian pit; basal impression narrow, closed posteriorly, open laterally; discal striole relatively wide, extending to middle of pronotum; marginal groove visible in dorsal view; angular seta present; three or four marginal setae, mostly anterior to middle; one or two anterior discal setae; no posterior discs; sternopleural groove absent; precoxal setae absent.

Elytra elongate; striae impressed, pollinose, coarsely punctate; apex of intratubercular stria rather shallow; preapical tubercle inflated, rounded; apical tubercles inflated, contiguous; sutural striole with complete row of five to seven setae;

parasutural stria with complete row of five or six setae; intercalary stria with about 13 setae; intratubercular stria with about five setae in apical 0.33; marginal stria with complete row of about 15 setae; apical tubercle with two setae; metasternum with very shallow median groove; Sterna II-VI with shallow transverse sulci, each containing row of coarse punctures; transverse sulci broadly interrupted in midline; Sternum VI without submarginal sulcus; four setae near posterior margin of Sternum VI (Fig. 147); in most specimens two setae near middle of Sternum VI, one specimen with three, another with four; female with deep lateral pit on Sternum IV, shallower one on Sternum V; false spur present, 0.67 as long as true spurs; male without ventral tooth on anterior femur, without proximal tooth on anterior tibia; calcaria short, broadly triangular, hind one deeper but not longer than middle one; dorsal margins of calcaria not angulate.

The very shallow frontal grooves on the head and the absence of the submarginal sulcus of Sternum VI are characteristic of this species. The shorter, more rounded pronotum with shorter discal striae also separates it from the sympatric *C. pilosum*. The complete series of setae in the parasutural stria also differentiates the type series from the latter species. However, this character is lacking in a specimen from Trujillo State, which may be a variant of *C. jolyi* (see below, under "variation").

Range and variation.— The type series is known only from Merida State. We have studied a female specimen, labelled: "Venezuela-Trujillo, La Peña, 3000 m., 5-IX-1968, J. & B. Bechyne" (VEN). This specimen is closer to *C. jolyi* in most respects, including the shape of the pronotum and the sculpture and chaetotaxy of Sternum VI. However, the elytral striae are distinctly finer, and the chaetotaxy of the pronotum and elytra differ in important respects: four temporal setae, six to eight marginal setae on the pronotum; parasutural stria without setae, and pilose apical bands only on antennal Segment I. This specimen might be an extreme variant of *C. jolyi*, although we suspect it is more likely to be a closely allied but distinct form. A final decision will need to await the collection of more specimens.

Clinidium (sensu stricto) oberthueri Grouvelle 1903

(Fig. 141)

Clinidium oberthueri Grouvelle 1903: 128-129.

Clinidium (sensu stricto) oberthueri (Grouvelle) Bell and Bell 1978.

Type Material.— LECTOTYPE (here designated) male, labelled: "Ecuador, coll. Slemiradsky 1882-1883" (MNHN). PARALECTOTYPES, seven specimens, sexes not recorded, same label as lectotype (MNHN); one male, one female, same data as lectotype, labelled "Co-type" (BMNH).

Description.— Length 6.0-6.3 mm. Antennal stylet slender, acuminate about 0.20 of length of Segment XI; latter long, conical; minor setal tufts on Segments V-X; basal setae present, but very sparse, on Segments VI-X; Segment I with broad subapical band of pollinosity; antenna otherwise without pollinosity; head distinctly longer than wide; frontal grooves narrow, shallow, margins inconspicuously pollinose; median lobe short, triangular, tip slightly behind anterior margin of eye; medial margins of temporal lobes slightly divergent posteriorly; posterior margin rounded, with narrow pollinose margin; eye narrowly crescentic, short, about 0.25 of length of temporal lobe; orbital groove complete, pollinose; lateral margin of head oblique posterior to eye; four temporal setae in orbital groove; two pairs of postlabial setae.

Pronotum elongate, length/greatest width 1.67, oval, base, apex strongly narrowed, lateral margin strongly curved, base nearly evenly rounded; apex narrowly truncate; median groove narrow, margins nearly parallel, dilated very slightly opposite anterior median pit; basal impression very narrow, closed posteriorly, open laterally; impression only slightly wider than discal stria, latter extending nearly to middle of pronotum; marginal groove visible in dorsal view; angular seta present; seven or eight marginals; one anterior discal or absent; notopleural suture dilated, pollinose near middle; sternopleural groove present; precoxal seta present.

Elytra moderately elongate, humeral region very strongly narrowed compared to related species; striae impressed, pollinose, coarsely punctate; apex of intratubercular stria rather shallow; all striae entire; preapical tubercle strongly inflated, rounded; apical tubercles weakly inflated, contiguous; sutural striae with complete row of four or five setae; parasutural stria without setae; intercalary stria with complete row of five to six setae; intratubercular stria with four or five setae in apical 0.20; marginal stria with 10-13 setae in complete row; preapical tubercle with four or five setae; apical tubercle with two setae; metasternum with deep median sulcus; transverse sulcus of Sternum III continuous in both sexes; that of Sternum IV narrowly interrupted in both sexes; V narrowly interrupted in male, widely interrupted in female; that of VI widely interrupted in both sexes; submarginal groove short, broadly separated from transverse sulci; female with eight setae on Sternum VI, four in curved lines near hind margin, four in transverse line near middle; male with six setae, inner pair of transverse line absent; female with very large lateral pit on Sternum IV; false spur absent, replaced by obtuse

angle; male without ventral tooth on anterior femur or proximal tooth on anterior tibia; middle calcar broadly triangular, dorsal margin straight; hind calcar larger, its apex obtuse, dorsal margin angulate.

The oval pronotum and very narrow elytral humeri of this species are distinctive. The precoxal setae also differentiate it from all members of the section except for *C. allenii*. The latter species has a shorter pronotum with more parallel margins, and linear discal striae.

Range.— Ecuador. The only specimens with a definite locality are three labelled: "Papallacta, Napo-Pastaza Prov., 30 January 1958, R. W. Hodges, 10500 ft. elev." (MSU; UVM). This is on the eastern side of the Andes.

Clinidium (sensu stricto) allenii new species
(Figs. 142, 148, 149)

Type Material.— HOLOTYPE male, labelled: "Panama, Cerro Jefe, 9° 12' N-79° 21' W, 700-750 m., May 20, 1972, beating and under bark. R. T. Allen, ADP 11544" (NMNH). This locality is in the Cordillera de San Blas, on the eastern, or South American side of the Panama Canal.

Description.— Length 6.4 mm. Antennal stylet very slender, inconspicuous, about 0.2 of length of Segment XI; latter short, nearly spherical; minor setal tufts on Segments V-X; basal setae entirely absent; Antennal Segments I-VI with pollinose subapical bands; more distal segments with pollinosity limited to bases of setae, forming broken bands; head 1.5 times longer than wide; frontal grooves narrow, deep, partly pollinose; median lobe short, triangular; joined to antennal lobe, tip opposite anterior margin of eye; medial margins of temporal lobes divergent posteriorly; posterior margin narrowly rounded; posterior and posteromedial margins broadly bordered with pilosity, so glabrous part of temporal lobe is strongly narrowed posteriorly; eye narrowly crescentic, about 0.33 of length of temporal lobe; orbital groove complete, pollinose; lateral margin of head nearly straight posterior to eye; three temporal setae in orbital groove; two pairs of postlabial setae.

Pronotum rather short, length/greatest width 1.40, widest just posterior to middle; base, apex moderately narrowed; lateral margin curved, apex truncate; base rounded; median groove narrow, margins pollinose, anterior median pit very small, but distinctly wider than median groove; basal 0.3 of median groove shallow, linear, glabrous; basal impression very small, deep, punctiform, sharply distinct from discal striae, latter linear, slightly curved, extending slightly anterior to middle of pronotum; marginal groove fine, visible in dorsal view; angular seta present; nine or 10 marginal setae; one or two anterior discal setae; sternopleural groove absent; precoxal setae present.

Elytra rather short; humeri much less narrowed than in *C. oberthueri*; intratubercular stria impressed only at base, apex, in middle represented only by row of punctures (Fig. 149); remaining striae impressed, entire, pollinose, coarsely punctured; Intervals II, III forming prominent swelling just posterior to base of elytron (this asymmetrical, and possibly the result of an injury); preapical tubercle inflated, rounded; apical tubercles inflated, rounded, slightly separated; sutural stria with complete row of five setae; parasutural stria with one or two setae near base; intercalary stria with complete row of six or seven setae; intratubercular stria with two or three setae near apex; marginal stria with complete row of about 12 setae; preapical tubercle without setae; apical tubercle with three or four setae; metasternum with very shallow median sulcus; transverse sulci of all abdominal sterna interrupted in midline, submarginal sulcus of Sternum VI widely separated from transverse sulci (Fig. 148); Sternum VI with four setae in submarginal row; one or two on each side in transverse row; middle, hind tibiae each with false spur; male without ventral tooth on anterior femur, without proximal tooth on anterior tibia; calcars triangular, middle one narrow, with dorsal margin straight; hind one broader, dorsal margin nearly straight. Female unknown.

This species resembles *C. oberthueri* in having precoxal setae, but differs from the latter in having a shorter, less rounded pronotum, elytral humeri much less narrowed, and discal striae and frontal grooves much shallower and narrower. *C. whiteheadi* is a similar species, found nearby, but to the west of the Panama Canal. It lacks the precoxal setae, has basal setae on the outer antennal segments, and has straight discal striae and a more parallel-sided pronotum.

We take pleasure in naming this species for Dr. R. T. Allen, whose collections have helped greatly in making known the beetle fauna of lower Central America.

Clinidium (sensu stricto) whiteheadi new species
(Fig. 143)

Type Material.— HOLOTYPE male, labelled: "PANAMA: Panama, Cerro Campana 8° 40' N, 79° 56' W, 29 June 74, 850 ms; T. L. Erwin, D. R. Whitehead, under loose bark of log; Exped #I 23, notebook #3, ADP 25285"

(NMNH). This locality is to the west of the Panama Canal, towards Central and North America. PARATYPES two males, three females, same label as holotype (NMNH); one female, same locality, collected by T. L. Erwin and J. L. Lawrence, 22 Feb. 1975 (in heartwood) (NMNH); one male, one female, same locality as holotype, labelled: "19-VIII-78, ex *Stemonitis*, Q. D. Wheeler 7867" (CU).

Description.—Length 5.0–5.8 mm. Antennal stylet minute, less than 0.1 of length of Segment XI; latter only slightly longer than wide; minor setal tufts on Segments V–X; basal setae present on Segments VIII–X; Segments I–IV with subapical pollinose bands; head slightly longer than wide, less elongate than in *C. alleni*; frontal grooves narrow but deep, pollinose; median lobe short, triangular, joined to antennal lobe; tip opposite anterior 0.25 of eye; medial margins of temporal lobes divergent posteriorly; posterior margin more broadly rounded than in *C. alleni*, posterior, posteriomedial margins broadly bordered with pilosity; eye narrowly crescentic, 0.33 of length of temporal lobe; orbital groove complete, pollinose; lateral margin of head nearly straight posterior to eye; two or three temporal setae in orbital groove; two pairs of postlabial setae.

Pronotum rather short, length/greatest width 1.54, widest near middle, lateral margins nearly straight; base, apex less narrowed than in *C. alleni*; apex truncate; base rounded; median groove narrow, though broader in *C. alleni*, widest in middle 0.33, slightly constricted near apex; not broadened at anterior median pit; posterior 0.33 very shallow, finely pollinose; basal impression very small, deep, punctiform, sharply distinct from discal striole; latter linear, straight, extending to middle of pronotum; marginal groove fine, visible in dorsal view; angular seta present; seven to nine marginals; one or two anterior discal setae; notopleural suture glabrous; sternopleural groove absent; precoxal setae absent.

Elytra rather short, humeri only slightly narrowed; intervals less convex than in *C. alleni*; intratubercular stria impressed only at base, apex; middle part, a row of fine punctures; remaining striae impressed, entire, pollinose, coarsely punctured; no swelling in Intervals II, III near base; preapical tubercle scarcely inflated, rounded; apical tubercles scarcely inflated, rounded, slightly separated; sutural stria without setae in most specimens, with one seta on one elytron in one female specimen; parasutural striae with one seta near base; intercalary stria with complete row of six or seven setae; intratubercular stria with three setae near apex; marginal stria with complete row of about 10 setae; preapical tubercle without setae; apical tubercle with two or three setae; metasternum with shallow median sulcus; transverse sulci of abdominal Sterna II–VI widely interrupted in midline; submarginal sulcus of Sternum VI widely separated from transverse sulci; Sternum VI with six to eight setae, four in row along submarginal sulcus, two on disc, in one male, with four on disc, lateral ones more anterior than medial ones; female with large lateral pit in Sternum IV; middle, hind tibiae each with large false spur; male without ventral tooth on anterior femur nor proximal tooth on anterior tibia; calcaria triangular, dorsal margins slightly curved; penis of holotype mounted separately on point, distal 0.5 straight, apex abruptly deflexed.

This species has linear, straight discal striae and a parallel-sided pronotum. This and the absence of precoxal setae separate it from *C. alleni*. *C. dormans*, another similar Panamanian species, has the apex of the intratubercular stria not impressed, so that preapical and apical tubercles are not separate.

We take pleasure in naming this species for Dr. Whitehead, one of the ablest and most productive of the students of Latin American beetles.

Bionomics.—The specimens were collected by Mr. Wheeler (*in litt.*) in the fruiting bodies of the slime mold *Stemonitis*. To our knowledge, this is the first record of a rhyzodine in a fruiting body, and the first linkage of a particular species of rhyzodine with a particular genus of slime mold.

Clinidium (sensu stricto) humboldti new species
(Figs. 144, 150)

Type Material.—HOLOTYPE female, labelled: "nov. Granad., 43693 (MNHB).

Description.—Length 6.4 mm. Antennal stylet about 0.25 of length of Segment XI, larger than in related species; Segment XI distinctly longer than wide; tufts of minor setae on Segments V–X; basal setae present on Segments VI–X; Segments I–VI with subapical pollinose bands; head distinctly longer than wide; frontal grooves rather broad, moderately deep, glabrous except for medial margins; median lobe short, triangular, tip opposite anterior 0.25 of eye; median lobe separated from antennal lobe by frontoclypeal groove; medial margins of temporal lobes slightly divergent posteriorly; glabrous area of temporal lobe oval, widest posterior to eye; posterior, posteriomedial margins broadly bordered by pollinosity; eye narrowly crescentic, elongate, 0.67 of length of temporal lobe; orbital groove complete, broadly pollinose; 4 temporal setae; two pairs of postlabial setae.

Pronotum rather short, length/greatest width 1.47, widest near middle, lateral margins strongly curved; base, apex strongly narrowed; apex truncate; base rounded; median groove slightly dilated; 0.75 deep, posterior 0.25 shallow; median groove not widened at anterior median pit; latter far posterior to pronotal apex; basal impressions small, deep, sharply

distinct from discal striole; latter linear, slightly curved, extending to middle of pronotum; basal impression broadly joined laterally to marginal groove; latter fine, visible in dorsal groove; angular seta present; seven or eight marginal setae; one pair of anterior discal setae; notopleural suture glabrous; sternopleural groove absent; precoxal setae present.

Elytra rather short, humeri scarcely narrowed; elytral intervals nearly flat; intratubercular stria impressed at apex; remainder scarcely impressed, represented by row of fine punctures; remaining striae impressed, entire, pollinose, coarsely punctate; no swelling on Intervals II, III near base; preapical tubercle strongly inflated, medial margins sinuate, apex subtruncate (Fig. 150); apical tubercle inflated; sutural stria with three or four setae in posterior 0.67; parasutural stria without setae; intercalary stria with complete row of nine or 10 setae; intratubercular stria with four or five setae near apex; marginal stria with 11-12 setae; preapical tubercle with one seta on medial margin; apical tubercle with three or four setae; metasternum with very shallow glabrous median impression, latter containing two elongate pits, near anterior, posterior margins, respectively; transverse sulci of Sterna III-VI linear, widely separated in midline, those of Sternum V slightly oblique; female with lateral pit on Sternum IV; transverse sulci of Sternum VI widely separated from submarginal sulcus; Sternum VI with eight setae; four in transverse row anterior to submarginal sulcus, four near posterior margin; middle, hind tibiae with short, triangular cusp, which does not resemble a spur. Male unknown.

This species resembles *C. whiteheadi* and *C. alleni* in appearance. It differs from both in having the median lobe not connected to the antennal lobes. It differs from *C. alleni* in the presence of basal setae on the antennae, in the shape of the temporal lobes, and in the presence of anterior discal setae. *C. whiteheadi* lacks precoxal setae, and has the pronotum more elongate, with the margins less curved.

We dedicate this species to Alexander von Humboldt and to the museum named for him, in gratitude for the loan of their valuable collection of Rhysodini.

THE JAMAICENSE SECTION

Like the preceding section, this one contains species with both intercalary and intratubercular striae with apices complete. However, there is no trace of a median sulcus on the metasternum. There are five species, two in Jamaica, and three in Hispaniola.

Phylogeny.— *C. trionyx* of the Dominican Republic contrasts strongly with the four remaining species. It has precoxal setae and false spurs, both probably plesiomorphic characters, in which it resembles some members of the *oberthueri* section. The eye is reduced to a small vestige, the discal strioles are absent, and the intratubercular stria is virtually absent except for its impressed apex. These are specialized features in comparison to the character states in the remaining species. The latter are very close to one another, and can be regarded as a species complex.

In the *jamaicense* complex, the two Haitian species clearly form one unit, and the two Jamaican ones, another unit.

Clinidium (sensu stricto) trionyx new species (Figs. 151, 160, 161)

Type Material.— HOLOTYPE male, labelled: "Rep. Dominic, J. & S. Klapperich, Cazabita 1250 m. 30-VI-74" (BSL).

Description.— Length 6.0 mm. Antennal stylet minute; minor setal tufts on Segments V-X; basal setae absent; antennal Segments I-IV with subapical pollinose bands; head slightly longer than wide; frontal grooves narrow, shallow, glabrous; median lobe triangular, rather long, tip opposite posterior margin of eye; medial margins of temporal lobes slightly convergent posteriorly; posterior margin rounded; posterior, posteriomedial margins bordered by pollinosity; eye minute, oblong, 0.2 of length of temporal lobe, eye 2.5 longer than deep (Fig. 161); orbital groove complete, pollinose; lateral margin of head slightly oblique posterior to eye; 3 temporal setae in orbital groove; one pair of postlabial setae.

Pronotum rather short, length/greatest width 1.47; widest just posterior to middle, oval, lateral margins curved; base curved; apex narrowly truncate; median groove narrow, margins pollinose, groove slightly dilated in middle 0.33; groove not at all dilated at anterior median pit; basal 0.33 of median groove shallow, pollinose; basal impression small, deep, triangular, closed posteriorly; discal striole absent; marginal groove fine, visible in dorsal view; angular seta present; five or six marginals, one pair of anterior discal setae; sternopleural groove absent; precoxal setae present.

Elytra relatively short, broad; three inner striae impressed, pollinose, entire; intratubercular stria with apex impressed, separating preapical from apical tubercle, remainder of intratubercular stria nearly absent, represented by faint impression visible by oblique lighting, without punctures or pollinosity; marginal stria entire, impressed, pollinose; preapical tubercle only slightly inflated; apical tubercles inflated, contiguous, meeting in straight median suture; sutural striae with complete row of five setae (most posterior one in apical impression just posterior to apex of sutural stria); parasutural stria with one seta at base; intercalary stria with complete row of six setae; apical impressed part of intratubercular stria with three setae, anteriormost one in conspicuous pollinose puncture; marginal stria with one seta near humerus, six or seven setae in apical 0.67, three or four in conspicuous punctures; metasternum without median sulcus; transverse sulci of abdominal Sterna III-VI widely separated in midline, also from margin, forming pairs of oval impressions, most with one or two small punctures medial to them; Sternum VI with submarginal groove widely separated from transverse sulci (Fig. 160); Sternum VI with four pairs of setiferous punctures, anterior ones in recurved row, posterior ones in procurved row along submarginal groove; middle, hind tibiae each with false spur; male without ventral tooth on anterior femur nor proximal tooth on anterior tibia; middle calcar narrowly triangular, close to spurs; hind calcar more broadly triangular, raised above level of spurs.

This species differs from the two Haitian members of the section in having slightly convergent temporal lobes, much more finely punctate striae, the intratubercular stria almost absent except for the impressed apex, a much smaller eye, precoxal setae and false spurs present. In the *oberthueri* group, it is closest to *C. alleni*, but differs in having only one pair of postlabial setae, metasternum not at all sulcate, and the discal striole absent.

THE *JAMAICENSE* COMPLEX

This includes *C. haitiense*, *C. corbis*, *C. jamaicense* and *C. chiolinoi*, in short, all members of the *jamaicense* section, excepting *C. trionyx*. The species are so similar that it is convenient to present a description for the complex before listing the distinctive features of each species.

Description.— Antennal stylet minute; minor setal tufts on Segments V-X; head distinctly longer than wide; orbital groove complete; eye narrowly crescentic, 0.5-0.67 of length of temporal lobe; cornea clear in some (younger?) specimens, completely darkly pigmented in other specimens; three temporal setae in orbital groove in most specimens, in some, one side has two or four setae; one or two pairs of postlabial setae, pronotum rather short, widest in middle, lateral margins curved, base rounded; apex truncate; median groove narrow, oval, pollinose, not at all dilated opposite anterior median pit; basal impression small, deep, triangular; closed posteriorly; discal striole varying among the species; marginal groove fine, visible in dorsal view; angular seta present; marginals two to six; one to three anterior discal setae; sternopleural groove, precoxal setae absent.

Elytra shorter, broader than in *C. trionyx*; striae coarsely punctured; inner three striae deeply impressed, pollinose, entire; intratubercular stria with apex impressed, remainder very shallowly impressed, but with coarse, conspicuous row of punctures; marginal stria entire, impressed; preapical tubercle scarcely inflated; apical tubercles slightly inflated, contiguous, meeting in straight median suture; metasternum not sulcate; transverse sulci moderately separated in midline, reaching to lateral margins of abdominal sterna; Sternum VI with submarginal sulcus widely separated from transverse sulci; Sternum VI with six to eight setiferous punctures; middle, hind tibiae without false spurs; male without ventral tooth on anterior femur nor proximal tooth on anterior tibia.

These four species differ strongly from *C. trionyx* in the absence of false spurs and precoxal setae, and in having the intratubercular stria coarsely punctate.

Clinidium (sensu stricto) haitiense Bell 1970

(Fig. 152)

Clinidium (sensu stricto) haitiense Bell 1970: 322.

Type Material.— HOLOTYPE male, labelled: "La Visite, La Selle Range, Haiti, 5000-7000 ft., coll. P. J. Darlington, Sept. 16-23, 1934" (MCZ 31755). PARATYPES one male, two females, same label as type (MCZ; UVM).

Description.— Length 5.7-6.4 mm. Antennae very thick; basal setae present on Segments VII-X or VIII-X; Segments I-II with complete subapical pollinose rings; Segments III, IV with rings interrupted; outer segments without pollinosity; median lobe of head long connected laterally to antennal lobes, tip of medial lobe opposite posterior margin of eye; frontal grooves deep, narrow, medial, lateral margins both sharp; margins of frontal grooves not pollinose; occipital pilosity short; orbital groove very narrow; head lateral to orbital groove behind eye glabrous; labium not pollinose medially.

Pronotum relatively elongate; length/greatest width 1.52; apex of pronotum more narrowed anteriorly than in *C. corbis*; discal setae in conspicuous punctures; in most specimens, two pairs of discals, forming rectangle, in one specimen one on one side, in another, three on one side; three to seven marginal setae; basal impression very narrow; discal striae in most specimens extending to posterior 0.25 of pronotum, but in one specimen, almost absent; pollinosity of discal striae much reduced.

Elytra relatively elongate with humeri slightly narrowed; Interval I slightly less convex than Intervals II, III; marginal coarsely punctate; sutural stria with three or four setae, mostly posterior to middle; parasutural without setae; intercalary with complete row of five to seven, intratubercular with two or three near apex; marginal stria with nine or 10 setae, one at humerus, others in posterior 0.5; apical tubercle with two or three setae; anterior femur with small pollinose spot at base of each seta; legs relatively long, slender; calcaria very small; hind calcar slightly obtuse, lower margin evenly curved.

This species is larger and more elongate than the closely related *C. corbis*, also from Haiti. It has the pilosity much reduced, with the dorsal surface of the femora with isolated pollinose spots at the bases of the setae, and the side of the head laterad to the orbital groove glabrous.

Range.— Probably restricted to high elevations in the Morne La Selle, south of Port-au-Prince. Bell (1970) recorded it from Furcy and Mandeville in addition to the type locality.

Clinidium (sensu stricto) corbis Bell 1970

(Fig. 153)

Clinidium (sensu stricto) corbis Bell 1970: 322-323.

Type Material.— HOLOTYPE male, labelled: "Tardieu, Morne La Hotte, Haiti, 3000 ft., coll. P. J. Darlington, October 14, 1934" (MCZ 31754). PARATYPES one female, same label as male (MCZ); one male, labelled: "Roche Croix, 5000 ft., Morne La Hotte, coll. P. J. Darlington, Oct. 13, 1934" (MCZ); two males labelled: "northeast foothills, Morne La Hotte, 2000-4000 ft., coll. P. J. Darlington, Oct. 10-24, 1934" (MCZ).

Description.— Length 4.4-5.5 mm. Antennae less thick than in *C. haitiense*, with the segments more nearly round; basal setae present, though sparse on Segments IX, X; Segments I-VIII in most specimens with subapical band of pollinosity; in a few specimens, pollinosity restricted to I-VI or I-VII; median lobe of head long, separated laterally from antennal lobes; tip of median lobe opposite posterior margin of eye; frontal grooves deep, narrow, margins pollinose; medial, lateral margins equally pollinose; orbital groove relatively broad; occipital pilosity prominent; head laterad to orbital groove posterior to eye pilose; labium with median pollinose band.

Pronotum relatively elongate, length/greatest width about 1.51; discal setae in smaller punctures than in *C. haitiense*, one or two pairs, varying geographically; four to six marginal setae; basal impression very narrow; discal striae longer, more pollinose than in *C. haitiense*, 0.30-0.50 of length of pronotum except in specimens from Dajabon, P.R.

Elytra in most specimens shorter than those of *C. haitiense*, Interval I slightly less convex than Interval II; marginal stria coarsely punctate; sutural stria with two or three setae posterior to middle; parasutural stria in most specimens without setae, in a few, with one seta at base; intercalary stria with complete row of five or six setae; intratubercular stria with one to three setae near apex; marginal stria with five-10 setae, including one at humerus; apical tubercle with two or three setae; anterior femur with dorsal pollinose stripe containing most of the setal bases; legs shorter, thicker than in *C. haitiense*; calcaria slightly larger than in *C. haitiense*; hind calcar acute, ventral margin abruptly bent.

This species is most easily separated from *C. haitiense* by the long pilosity laterad to the posterior part of the orbital groove.

Range.— This species is probably not confined to the Morne La Hotte, as supposed by Bell (1970). Specimens apparently belonging to this species have been found in the following additional localities: HAITI, Lebrun, near Miragoane, coll. R. T. Bell, R. Sette, over fifty specimens (UVM); Morne Grand Bois, 3780', coll. M. Langworthy, five specimens (UVM); Catiché, 2700', coll. M. Langworthy, one specimen (UVM); Ile de la Tortue, Aux Basin, w. of Aux Palmiste, coll. M. Langworthy, T. Dowhan (UVM). All localities except the last are from the Southern Peninsula: DOMINICAN REPUBLIC: Dajabon, Mariano Cestero, 650 m. 12-VIII-1980, A. Norrbom (CMP), two specimens. Probably this species was formerly throughout Hispaniola at low and medium elevations. One male and two females labelled: "WM 5958, Cinnamon Bay, June 6, 1980, between buttresses of large kapok tree" appear to represent this species, although they are unusually large, 5.0-5.6 mm. This locality is in the (American) Virgin Islands, on Saint John. They may represent an introduction by human agency, or a very recent natural invasion. The latter seems unlikely, in view of the apparent absence of the species from Puerto Rico. The specimens were collected by William Muchmore and sent to us by Kenneth Cooper.

Variation.— On the basis of the limited material available, the species appears to vary geographically, and might represent more than one taxon. In the type series, from Morne La Hotte, three have the discal setae on the pronotum 1-1 (one on each side), while two have them 1-2. The long series from Lebrun mostly have more discal setae. They are distributed as follows:

Discal setae	Number of specimens
1-1	9
1-2	13
2-2	22
2-3	4
3-3	1
2-1	1
3-1	1

In addition, the series from Lebrun appear to have the lateral margins consistently straighter and more parallel than specimens from other regions. The calcars appear identical to those from Morne La Hotte.

The series from Ile de la Tortue resemble those from Morne La Hotte in the shape of the pronotum and in having few discal setae. These are distributed as follows:

0-1	1 specimen
1-1	5
1-2	6

The hind calcar is scarcely raised above the level of the spurs.

The specimens from Dajabon, Dominican Republic, have the calcars as in the series from Morne La Hotte, which they also resemble in the shape of the pronotum. The discal setae are 1-1 and 0-1. The discal striae are much shorter than in other specimens of *C. corbis*, being scarcely longer than those of *C. haitiense*.

The specimens from Saint John have three or four discal setae, and have the calcar strongly raised above the tibial spurs. The length of the body is greater than those of the other series.

The differences among these populations may represent subspecific characters. However, they might be merely the result of individual variation. The large series from Lebrun were almost entirely from a single log. Two individuals were from a smaller piece of wood only a few meters away. Thus, the entire series could represent the offspring of a single mating. The same is true of the series from Ile de La Tortue.

Bionomics.— The series from Lebrun were mostly in small rotten areas in a large, dry, hard log. The local name of the tree is “marron”, but we were unable to find its scientific name. Two of the beetles were in a stick of *Cecropia* located a few meters away.

The series from Ile de La Tortue were in an unusual habitat, within a log in a sink hole in a large cave system.

Clinidium (sensu stricto) jamaicense Arrow 1942
(Figs. 154, 158)

Clinidium jamaicense Arrow 1942:181.

Clinidium (sensu stricto) jamaicense (Arrow) Bell and Bell 1978.

Type Material.— LECTOTYPE (here designated) male, labelled: “Jamaica, Dr. M. Cameron, BM-1936-555” (BMNH). According to the original description, the type series was collected at Newcastle, Jamaica, under rotting bark. PARALLECTOTYPES one male, two females, same label as lectotype. (BMNH).

Description.— Length 4.6-5.7 mm. Antenna with basal setae very few, confined to Segment X, or IX, X; Segments I-IV with subapical bands of pollinosity; median lobe of head short, blunt, opposite anterior 0.25 of eye; frontal grooves very shallow, glabrous; lateral margin of frontal groove ill-defined; occipital pilosity long; orbital groove broadly pollinose; labium pollinose medially.

Pronotum slightly shorter than in Haitian species, length/greatest width about 1.48; discal setae in most specimens one on each side, a few specimens with 2-1 or 0-1; marginal setae two or three, in most specimens with two near anterior angle, one near middle or absent; basal impression triangular, discal striae very short, shorter than basal impression, in many specimens obsolete.

Elytra relatively short, broad; Interval I narrow, convex, not broadened posteriorly; sutural stria deeply impressed, medial border as distinct as lateral border; parasutural stria deeply impressed, coarsely punctate; Intervals I-III of nearly equal height, convexity; intercalary stria deeply impressed; intratubercular stria with apex impressed, remainder a row of coarse punctures; marginal stria complete in all specimens; sutural stria with two or three setae near apex; parasutural stria without setae; intercalary stria with two to five setae, when numerous forming complete row; intratubercular stria with two or three setae in impressed apex; marginal stria with six or fewer setae, most anterior one at humerus; apical tubercle with two or three setae; calcar very small.

The shallow frontal grooves and short medial lobe distinguish this species from the two Haitian ones, while the convex sutural interval separates it from *C. chiolinoi*.

Range.— Mountains of Jamaica above 2000 ft. elevation. Bell (1970) recorded it from Portland Gap, Cinchona, Hardwar Gap, Blue Mountain Peak, Whitfield Hall, and Belmore Castle.

Clinidium (sensu stricto) chiolinoi Bell 1970
(Figs. 155, 159)

Clinidium (sensu stricto) chiolinoi 1970: 323-324.

Type Material.— HOLOTYPE male, labelled: “Mount Diablo, St. Ann Parish, Jamaica, coll. R. T., J. R. Bell, B. B. Chiolino, Jan. 2, 1967” (MCZ). PARATYPES two males, five females, same label as type (MCZ; UVM).

Description.— Length 4.4-5.6 mm. Antenna with basal setae on VI-X, VII-X, or VIII-X, sparse, mostly lateral; all antennal segments with subapical pollinose bands, those of distal segments very narrow; median lobe of head short, blunt, tip opposite anterior end of eye; frontal grooves very shallow, very finely margined with inconspicuous pollinosity; lateral margin of frontal groove ill-defined; occipital pilosity long; orbital groove broadly pollinose; labium pollinose medially.

Pronotum proportion as in *C. jamaicense*, length/greatest width 1.48; discal setae in most specimens one on each side, in a few specimens 2-1 or 1-0; marginal setae 2-3, in most specimens one or two near anterior angle, one near middle;

angular seta present or absent; basal impression triangular; discal striae very short, shorter than basal impression, in many specimens obsolete.

Elytra relatively short, broad, Interval I broad, flat, depressed below level of other intervals, wider posteriorly; sutural stria deep, punctate, medial margin lower than lateral margin; parasutural stria deeply impressed, punctate; intercalary striae shallowly impressed; Interval III more convex, higher than other intervals; intratubercular stria with apex impressed, remainder row of very fine punctures, in many specimens almost absent anteriorly; marginal stria entire (western specimens) or interrupted near humerus (eastern specimens); chaetotaxy of elytra identical to *C. jamaicense* except for five or six setae on apical tubercle; hind calcars very small.

This species resembles *C. jamaicense* but is easily separated by the strongly depressed Interval I (Fig. 159).

Range.—Jamaica, at elevations of 2000 ft. or less. Bell (1970) lists the following localities in addition to the type locality: John Crow Mountains, Port Antonio, Ocho Rios (Fern Gulley), Cornpuiss Gap, Belmore Castle.

Variation.—There is considerable variation among collections from various localities, and perhaps two or three subspecies will be recognized when more material is available. Specimens from western localities, Mt. Diablo, Fern Gulley, and Belmore Castle, have the parasutural and intercalary striae relatively shallow, and the marginal stria entire or nearly so. Specimens from the John Crow Mountains and Cornpuiss Gap have the parasutural and intercalary striae relatively deep and the marginal stria interrupted near the humerus. Specimens from Port Antonio resemble those from the John Crow Mountains in striation, but have first interval extremely flat and more widened posteriorly than in other populations.

Bionomics.—Bell (1970) collected this species in logs and sticks in relatively moist forest between sinkholes in the Karst Plateau of Mount Diablo. The locality at Fern Gulley is a very moist ravine only a few meters above sea level.

THE *ROSSI* SECTION

In this section, the intercalary stria is complete, but the apex of the intratubercular stria is absent, so that the preapical tubercle is not distinct from the apical tubercle. The median sulcus of the metasternum is variable. Except in *C. kochalkai*, the eye is reduced to a narrow line. There are five species, ranging from Costa Rica to western Venezuela.

Phylogeny.—*C. rossi* is probably the most isolated member of the section. In the absence of a metasternal sulcus, and the presence of only one temporal seta and a pair of crossed occipital setae, it differs from the remaining species.

The latter consists of two pairs of similar species. *C. dormans* and *C. penicillatum* lack discal setae, have short discal striae, only three temporal setae and two or three marginals, while the other pair, *C. segne* and *C. kochalkai*, have discal setae, long discal striae, four temporal setae and five or more marginals. Each of these pairs has one species with a linear median groove and precoxal setae present (*C. dormans*, *C. segne*) and another with a dilated median groove and without precoxal setae (*C. penicillatum*, *C. kochalkai*). Possibly these characters indicate the real phylogeny, and the preceding characters are the result of convergence. On balance, we believe that the converse is more likely true, that *C. dormans* is related to *C. penicillatum* and *C. segne* to *C. kochalkai*.

Clinidium (sensu stricto) rossi Bell 1970

(Fig. 156)

Clinidium (sensu stricto) rossi Bell 1970:321-322.

Type Material.— HOLOTYPE male, labelled: "Golfito, Costa Rica, Oct. 30, 1950, coll. E. S. Ross" (CAS).

Description.— Length 4.1 mm. Antennal stylet minute; antennae short, stout; tufts of minor setae on Segments V-X; basal setae not studied; head 1.5 longer than wide; frontal grooves very shallow, anterior portion obsolete; median lobe relatively narrow, triangular, tip opposite middle of eye; medial margins of temporal lobes parallel posteriorly; posteriomedial, posterior margins of temporal lobe broadly margined with pilosity; orbital groove complete; eye very narrow, linear, pigments in holotype; one temporal seta, in orbital groove posterior to eye; one pair of occipital setae present, crossed; one pair of postlabial setae.

Pronotum moderately long, length/greatest width 1.53; lateral margins parallel in middle 0.33, obliquely narrowed to base, apex; base rounded, apex truncate; median groove linear, not at all dilated at anterior median pit, narrowly dilated between middle and basal 0.25; basal impressions elongate, triangular, closed posteriorly; discal striole relatively short, reaching basal 0.33 of pronotum; marginal groove linear, visible in dorsal view; angular seta present; five marginal setae; one pair of anterior discals; sternopleural groove distinct, though shallow; precoxal setae absent.

Elytra relatively short, broad; sutural, parasutural, intercalary striae complete, impressed, finely punctate; intratubercular stria with apex not impressed, so preapical tubercle not distinct from apical tubercle; remainder of intratubercular stria coarsely punctate, very shallowly impressed; marginal stria complete, deeply impressed; sutural striae with four or five setae in complete row; parasutural stria without setae; intercalary stria with five or six setae in complete row; intratubercular stria without setae; marginal stria with 10 setae, forming complete row; apical tubercle with three setae, forming complete row; apical tubercle with three setae in line with intratubercular stria, one ventrad to them, near suture; metasternum without median sulcus; transverse sulci of abdominal Sterna III-VI broadly interrupted in midline; submarginal groove of Sternum VI widely separated from transverse groove; Sternum VI with six setae, four in transverse row in middle, two near submarginal groove; male without ventral tooth on anterior femur nor proximal tooth on anterior tibia; calcar very small; female with lateral pit on Sternum IV, shallower pit on Sternum V.

This species is easily recognized by the very shallow frontal grooves, the crossed occipital setae and the presence of only one temporal seta.

In addition to the type specimen we have seen one male, one female labelled: "Golfito, Costa Rica, July 7, 1957, Truxal & Menka" (LA).

Clinidium (sensu stricto) dormans new species
(Figs. 157, 162)

Type Material.— HOLOTYPE male, labelled: "Finca Lerida, near Boquete, Chiriquí Prov., Panama, Mar. 15, 1959, G. A. Salem leg. CNHM Panama Zoo. Exped. (1959) ADP 06974, La Barca, 5650'" (NMNH).

Description.— Length 5.2 mm. Antennal stylet minute; tufts of minor setae on Segments V-X; basal setae present on Segments VII-X; Segments I-III with subapical pollinose rings; head longer than wide; frontal grooves very shallow, glabrous; median lobe short, broad, triangular, tip even with middle of eye; medial margins of temporal lobes slightly divergent posteriorly; anterior part of frontal space glabrous, shallow; posteriomedial, posterior margins of temporal lobe margined with pilosity; orbital groove complete; eye very narrow, linear, 0.4 of length of temporal lobe; heavily pigmented in holotype; three temporal setae, two opposite eye, one posterior to eye; occipital setae absent; postlabial setae apparently absent (but possibly lost from holotype).

Pronotum moderately long, length/greatest width 1.47; lateral margins curved; apex truncate; base rounded; margin oblique anterior to hind angle; median groove narrow, margins nearly parallel, except for slight expansion at anterior median pit, constriction posterior to posterior median pit; basal impression elongate, triangular, discal striole relatively short; extending to posterior 0.33 of pronotum; marginal groove linear, visible in dorsal view; angular seta present; one or two marginal setae near apex of pronotum, also one just anterior to angular seta; discal setae absent; precoxal setae present, sternopleural groove absent.

Elytra moderately elongate, relatively broad; sutural, parasutural, intercalary striae complete, impressed, finely punctate; intratubercular stria virtually absent, represented by scattered, irregular punctures, preapical tubercle not separated from apical tubercle (Fig. 162); marginal stria impressed, apical 0.25 dilated; sutural stria without setae; parasutural stria with one seta at base; intercalary stria with complete row of five setae; marginal stria with one or two setae near middle, four in impressed apical portion; apical tubercle with two or three setae on medial margin, one in line with those of intercalary stria, also four or five arising from line of coarse punctures on lateral surface, probably representing posterior part of intratubercular stria; metasternum with shallow median sulcus; transverse sulci of abdominal Sterna narrow, shallow, broadly interrupted at midline; Sternum VI with submarginal sulcus widely separated from transverse sulci; Sternum VI with two pairs of setae, one on disc, other on submarginal sulcus; male without ventral tooth on anterior femur nor proximal tooth on anterior tibia; false spur absent, short, broadly triangular tooth in its place; middle calcar narrowly angular; hind calcar broadly triangular; both small. Female unknown.

This species is closest to *C. penicillatum* of Colombia, but the latter species has the median groove dilated in the middle 0.33, the frontal grooves deeper, precoxal setae absent, the discal striole scarcely evident, and the pronotum strongly narrowed anteriorly.

Clinidium (sensu stricto) penicillatum new species

(Figs. 163, 170)

Type Material.— HOLOTYPE female, labelled: "Colombia: Dept. Valle, 1967, R. B. Root, W. L. Brown, Represa Calima, below dam, 1200 m., 21 Mar., canyon bottom" (MCZ).

Description.— Length 6.0 mm. Antennal stylet small, 0.1 of length of Segment XI; tufts of minor setae on Segments V-X; basal setae present on Segments V-X; Segments I-VII with subapical pollinose rings; head 1.5 longer than wide; frontal grooves narrow, moderately deep, partly pollinose; median lobe short, broad, triangular, tip margined by pollinosity, even with anterior margin of eye, joined to antennal lobe; medial margins of temporal lobes slightly convergent posteriorly; posteriomedial, posterior margins of temporal lobe bordered with pollinosity; orbital groove complete; eye very narrow, linear, 0.4 of length of temporal lobe; three temporal setae, two opposite eye, one posterior to eye; occipital setae absent; one pair of postlabial setae.

Pronotum rather elongate, length/greatest width 1.57; greatest width near base; margins convergent anteriorly; apex narrow, truncate; base slightly narrowed, rounded; anterior 0.1, posterior 0.33 of median groove linear, middle portion narrowly dilated, conspicuously pollinose; basal impression elongate, triangular; discal striole scarcely evident; angular seta present; two or three marginals present, near apex, one at base; discal setae absent; precoxal setae absent; sternopleural groove absent.

Elytra moderately elongate; sutural, parasutural, intercalary striae complete, impressed, rather coarsely punctate; intratubercular stria nearly absent, represented by row of very fine punctures; preapical tubercle not separate from apical tubercle; marginal stria impressed, apical 0.25 dilated; sutural stria with one seta near apex; parasutural stria with one seta at base; intercalary stria with complete row of five setae; marginal stria with one seta near middle, two behind middle, and five or six near apex; apical tubercle with row of three or four setae on medial margin, row of six on lateral surface, in line with intratubercular stria; metasternum with shallow, broad median sulcus; transverse sulci of Sterna III-VI broadly interrupted in midline, each with row of fine punctures; Sternum VI with submarginal sulcus widely separated from transverse sulci; Sternum VI with eight setae, four in transverse row, four in curved row posterior to submarginal sulcus; female with shallow lateral pit on Sternum IV, very shallow one on Sternum V; false spurs absent; hind femur of female with dense brush of long pilosity on dorsal aspect (Fig. 170); male unknown.

This species is closest to *C. dormans* but differs in having the median lobe connected to the antennal lobe, in having the middle part of the median groove dilated, and the pronotum widest near the base and strongly tapered anteriorly. The brush on the hind femur is unique, but may be a secondary sexual character, as the male is unknown.

Clinidium (sensu stricto) segne new species

(Figs. 164, 173)

Type Material.— HOLOTYPE female, labelled: "VEN. Edo. Aragua, Rancho Grande, 1500 m. (15 km n. of Maracay), 21-11-1971, S. Peck" (BSRI). PARATYPE one female, same label as holotype (BSRI). The type locality is near the north coast of Venezuela, a little west of Caracas.

Description.— Length 4.6-5.2 mm. Antennal stylet very slender, 0.25 of length of Segment XI; tufts of minor setae on Segments V-X; Segments I-VII with subapical pollinose rings; basal setae on Segments IX-X or VIII-X, sparse; head slightly longer than wide; frontal grooves deep, narrow, median lobe short, triangular, tip opposite anterior part of eye; medial margins of temporal lobes slightly divergent posteriorly; posterior, posteriomedial margins of temporal lobe very broadly bordered by pilosity; orbital groove complete; eye narrow, short, about 0.3 of length of temporal lobe; four temporal setae, one anterior to eye, two opposite eye, one posterior to eye; occipital setae absent; two pairs of postlabial setae.

Pronotum moderately long, length/greatest width 1.47; widest slightly behind middle, lateral margins curved; apex narrowed, truncate; base moderately narrowed, rounded; median groove narrow, margins parallel, not at all expanded at anterior median pit; posterior 0.20 very narrow, shallow; basal impression narrow, triangular; discal striole linear, straight or slightly curved, extending 0.30 to 0.40 of length of pronotum; marginal groove slightly dilated, visible in dorsal view; angular seta present; nine or 10 marginal setae; two pairs of discal setae, more anterior ones near anterior margin, posterior ones slightly anterior to middle; precoxal seta present; anterior part of sternopleural groove faintly suggested; middle part absent.

Elytra moderately elongate; sutural, parasutural, intercalary striae complete, impressed, finely punctate; intratubercular stria shallowly impressed, base entire, apex effaced, so preapical tubercle not separate from apical tubercle (Fig. 173); marginal stria impressed, entire, apical 0.25 dilated; sutural stria with complete row of five setae; one seta in conspicuous puncture at anteriomedial angle of Interval III; intercalary stria with complete row of nine setae; intratubercular stria without setae; marginal stria with complete row of about 18 setae; apical tubercle with two setae on medial margin, row of five setae in isolated punctures on lateral surface, in line with intratubercular striae; metasternum with deep median sulcus; transverse sulci of Sterna III-VI narrow, impunctate, broadly separated in midline; submarginal sulcus of Sternum VI widely separated from transverse sulci; Sternum VI with six setae, two on disc, four posterior to submarginal sulcus; female with shallow lateral pit on Sternum IV, very shallow one on Sternum V; false spurs absent. Male unknown.

In chaetotaxy, in having a long discal striole and an impressed intratubercular stria, this species resembles *C. kochalkai*. In the latter species, the median groove is much more dilated, and there is at most one seta in the sutural stria.

Clinidium (sensu stricto) kochalkai new species
(Fig. 165)

Type Material.— HOLOTYPE male, labelled: "COLOMBIA 8860', J. A. Kochalka, Casa Antonia, Loma Cebolleta, S(ierra) N(evada) de Santa Marta, V-8-1975" (to be deposited in NMNH). PARATYPE female, same label as holotype (to be deposited in NMNH).

Description.— Length 6.0 mm. Antennal stylet very slender, long, 0.33 of length of Segment XI; tufts of minor setae on Segments V-X; Segments I-IV with subapical pollinose rings, V-VI with small pollinose spots; a few basals on Segment X; head slightly longer than wide; frontal grooves deep, broader than in *C. segne*; median lobe short, triangular, tip opposite anterior margin of eye; medial margins of temporal lobes slightly convergent posteriorly; margins of temporal lobe with much narrower pilose borders than *C. segne*; orbital groove complete; eye narrow, 0.5 of length of temporal lobe; three or four temporal setae in orbital groove, one or two at anterior margin of eye; one at its posterior margin, one posterior to eye; occipital setae absent; two or three pairs of occipital setae.

Pronotum moderately long, length/greatest width 1.43; widest near middle, lateral margins curved; apex, base moderately narrowed, apex truncate, base curved; median groove dilated, deep in middle, tapered anteriorly, not at all dilated at anterior median pit; posterior 0.25 linear, shallow; basal impression triangular, tapered gradually into discal striole, latter broader than in *C. segne*; discal striole attaining middle of pronotum; marginal groove dilated, prominent in dorsal view; six or seven marginal setae; one pair of anterior discal setae; precoxal setae absent; sternopleural setae absent.

Elytra rather broad; sutural, parasutural, striae complete, impressed, finely punctate; intercalary stria impressed, apex entire, but base abbreviated posterior to level of humerus; intratubercular stria shallowly impressed, apex effaced so preapical tubercle not separate from apical tubercle; marginal stria impressed, entire, apical 0.25 dilated; sutural stria without setae, or with one seta anterior to middle; anteriomedial angle of Interval III without seta; intercalary stria with complete row of seven or eight setae; intratubercular stria without setae; marginal stria with complete row of nine or 10 setae; medial margin of apical tubercle with five setae, lateral surface with four or five setae in conspicuous punctures aligned with intratubercular stria; metasternum with deep median sulcus; transverse sulci of Sterna III-V linear, broadly separated in midline; transverse sulci of Sternum VI dilated, oval broadly separated; submarginal sulcus of Sternum VI dilated, well separated from transverse sulci; Sternum VI with six setae, four posterior to submarginal sulci, two on disc, widely separated; anterior margin of submarginal sulcus evenly curved in male, angulate, slightly tuberculate in midline in female; female with shallow lateral pit on Sternum IV; middle hind tibiae without false spur, but with short, triangular tooth in its place; male without ventral tooth on anterior femur, without proximal tooth on anterior tibia; calcars raised above level of spurs; obliquely truncate.

This species is easily recognized by the dilated middle portion of the median groove of the pronotum and by the abbreviation of the base of the intercalary stria. It is named for the collector, the able and enthusiastic arachnologist, John A. Kochalka, our friend and former student.

THE *GUILDINGII* SECTION

In this section, the intercalary stria is abbreviated posteriorly, while the intratubercular stria is complete to the apex, separating the preapical tubercle from the apical tubercle. The metasternum lacks a median sulcus. The false spurs are well-developed. The section consists of

four species, each confined to one island in the Lesser Antilles.

Phylogeny.—Of the four species, *C. guildingii* is the most isolated, with the apical tubercles separated by a large, round space, and the female with Sternum VI with a median tubercle. The three remaining species have a small pore beneath the apical tubercle, which are broadly contiguous above it. Of these, *C. microfossatum* contrasts with the remaining two in the virtual disappearance of the intratubercular stria and the abbreviation of the marginal stria at the base. The femur of the male has many minute tubercles on the ventral surface, a feature not found in other members of the genus. *C. planum* and *C. smithsonianum* are closely related to one another, but differ in secondary sexual characters and in the length of the discal striole.

Clinidium (sensu stricto) guildingii Kirby 1835

(Figs. 167, 174, 176, 177)

Clinidium guildingii Kirby 1835: 8-10.

Rhyzodes guildingii (Kirby) Newman 1838. Chevrolat (1873a) changed the spelling to "guldingi", a practice followed by most later authors.

Clinidium (sensu stricto) guildingii (Kirby) Bell 1970.

Type Material.—We have not been able to locate type material for this species. The original description does not indicate the location of types, and the latter are not in the British Museum of Natural History. According to the description, the type locality is Mount Saint Andrews, Saint Vincent. We have studied two males and one female collected by ourselves at the type locality. If the type series is really lost, these could serve as neotypes.

Description.—Length 5.5-6.0 mm. Antennal stylet acuminate, 0.3 of length of Segment II; tufts of minor setae on Segments V-X; basal setae present on Segments VII-X or VIII-X; Segments I-VI with subapical bands of pollinosity; head slightly longer than wide; frontal grooves moderately deep, pollinose, of even width; median lobe short, broad, triangular, tip even with anterior part of eye; frontal space moderately broad; medial margins of temporal lobes oblique, slightly divergent posteriorly; posterior, posteriomarginal margins of temporal lobe bordered with pollinosity; orbital groove narrow, complete; eye narrowly crescentic, deeply pigmented in mature specimens; most specimens with three temporal setae, in orbital groove; a few specimens with two or four temporals; two pairs of postorbital setae.

Pronotum elongate, length/greatest width 1.49; lateral margins curved; apex strongly narrowed, base moderately narrowed; apex truncate; base rounded; margin oblique anterior to hind angle; median groove slightly dilated, margins parallel in middle, groove slightly enlarged at anterior median pit; basal 0.33 of groove narrow, shallow; basal impression narrow, triangular; discal striole long, attaining middle of pronotum; marginal groove visible in dorsal view; angular seta present, anterior, medial to hind angle; about 10 marginal setae present; discal setae, precoxal setae absent; sternopleural groove complete.

Elytra short, relatively broad; striae impressed, indistinctly punctate; intercalary stria abbreviated posteriorly; intratubercular stria complete; marginal stria complete; apical tubercles inflated, truncate posteriorly, touching at dorsoposterior points above large, round opening (Fig. 177); sutural stria with complete row of four or five setae; intercalary stria with complete row of six to eight setae; intratubercular stria with one seta at base, three near apex; marginal stria with about 17 setae; apical tubercle with three setae in prominent punctures; metasternum without median sulcus; male with transverse sulci of abdominal Sterna III-V complete, not interrupted in midline, with those of VI narrowly interrupted in midline, connected laterally to submarginal sulcus; female with sulci of Sterna III-IV complete, that of V narrowly interrupted; that of VI broadly interrupted; Sternum VI in both sexes with one pair of setae in submarginal sulcus; Sternum VI of female with median tubercle, disc sloped gradually posterior to it (Figs. 174, 176); male anterior femur without ventral tooth; male anterior tibia without proximal tooth; false spurs present on middle, hind tibiae; middle, hind calcaria triangular, not notched on dorsal margin.

The large circular opening between the apical tubercles is distinctive. The male has calcaria similar to those of *C. microfossatum*, but does not have tubercles on the ventral side of the anterior femur. The female differs from other known females in having a tubercle in the middle of Sternum VI.

Range.—St. Vincent, in the Lesser Antilles. We have studied two males and one female, labelled: "Checkley Level, Mount Saint Andrew, coll. J. R. Bell, Dec. 31, 1968" (UVM), and one female, labelled: "Richmond Est., Oct. 31, open valley, sea level in rotten wood, Kingstown" (collector and year not given) (BMNH).

There is one female labelled "Guadeloupe", which is clearly this species and not *C. planum*. We suspect that the locality label is incorrect.

Bionomics.— Bell (1970) describes in detail the situation of the specimens from Mount Saint Andrews. These were collected in the stump and roots of *Torrubia fragrans* (Du Mont de Courset), a member of the Nyctaginaceae.

Clinidium (sensu stricto) microfossatum new species
(Figs. 168, 171)

Type Material.— HOLOTYPE male, labelled: "La Martinique, Dr. L. Pornain, 1901" (MNHN).

Description.— Length 5.8 mm. Antennal stylet acuminate, about 0.3 of length of Segment XI; tufts of minor setae on Segments V-X; basal setae present on Segments VI-X or VII-X; Segments I-III with subapical bands of pollinosity; head distinctly longer than wide; frontal grooves deep, narrower than in *C. guildingii*, of even width, margined with pollinosity; median lobe short, broad, triangular, tip even with anterior part of eye; frontal space rather narrow; medial margins of temporal lobes oblique, slightly divergent posteriorly; posterior, posteriomedial margins of temporal lobe with very narrow pollinose borders; orbital groove very narrow, complete or with short interruption posterior to eye; eye narrowly crescentic; orbital groove with two temporal setae, one opposite eye, the other near posterior margin; two pairs of postlabial setae.

Pronotum elongate; length/greatest width 1.55; lateral margins curved; apex strongly narrowed, more so than in *C. guildingii*; base moderately narrowed; apex truncate; base rounded; margin oblique anterior to hind angle; median groove narrow, less dilated than in *C. guildingii*, margins parallel; groove very slightly dilated at anterior median pit; basal 0.33 very narrow, shallow; basal impression small, oval, discal striole absent; marginal groove visible in dorsal view, finer than in *C. guildingii*; angular seta medial, anterior to hind angle; five or six marginal setae; discal, precoxal setae absent; sternopleural groove effaced anteriorly.

Elytra short, relatively broad; sutural, parasutural, intercalary striae impressed, pollinose; intercalary stria abbreviated posteriorly; intratubercular stria not impressed, not pollinose, represented only by line of fine punctures, preapical tubercle thus scarcely separated from apical tubercle (Fig. 171); marginal stria incomplete, basal 0.25 entirely effaced, next 0.25 represented only by row of fine punctures; apical 0.5 impressed; apical tubercles inflated, truncate, meeting in straight line at suture, minute pore in midline below them; sutural stria with four or five setae in complete row; intercalary stria with complete row of eight setae; intratubercular with one seta at base, one at apex; marginal stria with about nine setae; apical tubercle with two setae in line with intratubercular stria; five setae in row ventrad to preceding; metasternum without median sulcus; male with transverse sulci of Sterna III, IV complete, that of V narrowly interrupted in midline, that of VI broadly interrupted in midline, widely separated from submarginal sulcus; Sternum VI with one pair of setae; male with anterior femur without ventral tooth, but with many minute tubercles on ventral surface; male without proximal tooth on anterior tibia; false spurs present; calcars triangular, dorsal margins straight, not notched. Female unknown.

The reduction of the intratubercular stria and of the base of the marginal stria are distinctive. The virtual absence of the discal strioles separates it from *C. smithsonianum* and *C. guildingii*. Some individuals of *C. planum* have the strioles equally reduced, but differ in the shape of the frontal space and, in the male, in the absence of tubercles on the ventral side of the anterior femur, and in the shape of the calcars.

Clinidium (sensu stricto) smithsonianum new species
(Figs. 169, 175, 178)

Type Material.— HOLOTYPE male, labelled: "Dominica: 2 mi. NW Pont Casse, X-26-1964, P.J. Spangler" (NMNH). Twelve PARATYPES: two females, same data as holotype (one specimen missing head and thorax) (NMNH); four females labelled: "Dominica, 3.0 mi. E. of Pont Casse, VII-31-1964, T.J. Spilman" (NMNH); one female labelled: "Dominica, 1.0 mi. E. of Pont Casse, VII-23-1964, T. J. Spilman" (NMNH); one male, one female labelled: "Dominica, 0.6 mi. W. of Pont Casse, VII-7-1964, T. J. spilman" (NMNH). (All the foregoing specimens also bear the label: "Bredin-Archbold Smithsonian Survey".); one male, one female, labelled: "Dominica, nr. Jean, 2000', 11-17-65, JFGC & T. M. Clarke, in rotten log" (NMNH); one female, labelled: "Wet Area Exp. Sta. St. Joseph Parish, 800', 31 Dec. 1978, M. A. & L. L. Ivie" (MAI).

Description.— Length 5.0-6.1 mm. Antennal stylet acuminate, about 0.3 of length of Segment XI; tufts of minor setae on Segments V-X; basal setae present on Segments V-X; Segments I-V with pollinose subapical bands; head distinctly longer than wide; frontal grooves deep, rather narrow, of even width, margined by pollinosity; median lobe short, broad, triangular, tip even with anterior part of eye; frontal space rather narrow; medial margins of temporal lobes oblique, slightly divergent posteriorly; posterior, posteriomedial margins of temporal lobes very narrowly bordered with pollinosity;

orbital groove very narrow, complete or with short interruption posterior to eye; eye narrowly crescentic; orbital groove with two temporal setae, one opposite eye, the other near posterior margin; two pairs of postlabial setae.

Pronotum moderately elongate; length/greatest width 1.50; lateral margins curved; apex strongly narrowed; base moderately narrowed; apex truncate; base rounded; margin oblique anterior to hind angle; median groove narrow, margins parallel; groove very slightly dilated at anterior median pit; basal 0.33 very narrow, shallow; basal impression small, triangular, discal striole well-developed, with basal impression about 0.35 to 0.40 of length of pronotum; marginal groove fine, visible in dorsal view; angular seta medial, anterior to hind angle; seven or eight marginal setae; discal, precoxal setae absent; sternopleural groove absent.

Elytra short, relatively broad; all striae impressed, pollinose; intercalary stria abbreviated posteriorly; marginal stria complete to base; apical tubercles inflated, truncate, meeting in straight line at suture, minute pore in midline below them (Fig. 178); sutural stria with complete row of four or five setae; intercalary with complete row of eight or nine setae; intratubercular stria with one seta at base, three or four setae in apical 0.33; marginal stria with 13-14 setae; apical tubercle with three setae in prominent punctures; metasternum without median sulcus; male with transverse sulci of Sterna III-V complete; transverse sulci of VI widely separated at midline, widely separated from submarginal sulcus; female with transverse sulci of Sterna III-IV complete; sulcus of V narrowly interrupted at midline; Sternum VI of female with transverse scarp at middle of length, scarp bounded posteriorly by deep oval impression, latter with central convexity, bounded laterally by longitudinal oval, pollinose cavity (Fig. 175); female with lateral pit on Sternum IV; both sexes with one pair of setae on Sternum VI, posterior to submarginal sulcus; false spurs present; male without ventral tooth or tubercles on anterior femur; male without proximal tooth on anterior tibia; calcars with dorsal margins weakly angulate.

The long discal striole gives this species a similarity to *C. guildingii*, but it differs from the latter species in having only a minute pore beneath the apical tubercles. *C. planum* is more closely related, but has shorter discal strioles, and differs in secondary sexual characters, the male having more strongly angulate calcars, and the female having the impression of Sternum VI without a central tubercle.

In addition to type material, we have seen two males labelled: "Dominica, St. Peter syndicate estate, under bark, 7-10-VII-1970, coll. J. H. Frank" (BMNH); one female, labelled: "Dominica, Springfield Est., VI-20-25-69, P. J. Darlington, Jr." (MCZ).

Clinidium (sensu stricto) planum (Chevrolat 1844)

(Figs. 166, 172)

Rhyzodes planus Chevrolat 1844: 58.

Clinidium guildingii Kirby (wrongly synonymized by Chevrolat 1873a).

Clinidium planum (Chevrolat) Arrow 1942.

Clinidium (sensu stricto) planum (Chevrolat) Bell 1970.

Type Material.— We have not been able to locate type material. We have studied a specimen from the type locality, Point-a-Pitre, Guadeloupe. It is a male, labelled: "Point-a-Pitre, Guadeloupe, W.I., June 6, 1911" (AMNH). If the type of *C. planum* is lost, this specimen could serve as a neotype. Another similar male specimen is labelled "Guadeloupe, Vitrac" (GEN).

Description.— Length 5.3-6.3 mm. Antennal stylet acuminate, 0.3 of length of Segment XI; tufts of minor setae on Segments V-X; basal setae present on Segments VI-X; Segments I-V with subapical bands of pollinosity; head slightly longer than wide; frontal grooves narrow, rather shallow, pollinose, narrowed near junction with frontal space; median lobe short, broad, triangular, tip even with anterior part of eye; frontal space rather narrow, anterior part with margins parallel, separated by more or less distinct angles from posterior part with oblique margins; posterior, posteromedial margins bordered by pollinosity; orbital groove very narrow, complete or with short interruption posterior to eye; eye narrowly crescentic, orbital groove with two temporal setae; one opposite eye; other near posterior end of orbital groove: two pairs of postlabial setae.

Pronotum moderately elongate; length/greatest width 1.51; lateral margins curved; apex narrowed; base only slightly less narrowed than apex; apex truncate; base rounded; margin oblique anterior to hind angle; median groove slightly dilated near middle, narrowed anteriorly, scarcely dilated at anterior median pit; basal 0.33 very shallow, narrow; basal impression small, triangular; discal striole relatively short, 0.1 to 0.25 of length of pronotum; marginal groove fine, visible in dorsal view; angular seta medial, anterior to hind angle; seven or eight marginal setae; discal, precoxal setae absent; sternopleural groove absent.

Elytra relatively short, broad; all striae impressed, pollinose; intercalary stria abbreviated posteriorly (Fig. 172); marginal stria complete to base; apical tubercles inflated, truncate, meeting in straight line at suture, minute pore in midline beneath them; sutural stria with complete row of four or five setae; intercalary stria with complete row of five to seven setae; intratubercular stria with one seta at base, three in apical 0.33; marginal stria with six to eight setae in

complete row, sparse near middle of length; apical tubercle with three setae in prominent punctures; metasternum without median sulcus; male with transverse sulcus of Sternum III complete, those of III, IV complete in some specimens, narrowly interrupted in others; that of V narrowly separated; female with transverse sulci of Sterna III-V not interrupted; female with deep lateral pit on Sternum IV and shallow one on Sternum V; in both sexes, Sternum VI with submarginal sulcus widely separated from transverse sulci; one pair of setae, posterior to transverse sulcus; female with transverse scarp on Sternum VI, bounded posteriorly by deep, entirely pollinose impression without median convexity; scarp in lateral view forming right angle with anterior part of disc; false spur on middle and hind tibiae present; male without ventral tooth or tubercles on anterior femur, without proximal tooth on anterior tibia; calcars strongly angulate on dorsal margin; margin distinctly notched between angle and shaft of tibia.

The discal striae of this species are intermediate in length, separating it from *C. guildingii* and *C. smithsonianum*, which have long ones, and probably from *C. microfossatum* which almost lacks them. The male is also distinguished by the strongly notched dorsal margin of the hind calcar, and the female by the deep pollinose impression of Sternum VI.

Range.— Probably confined to Guadeloupe. We have seen several specimens labelled "W. Ind." (MNHN) that appear to belong to this species. In addition we have seen a specimen labelled "Mexico, Bowditch" (MCZ) that is either *C. planum* or else another species closely related to it. It is a female which resembles *C. planum* except that the impression of Sternum VI is not pollinose, and the disc of Sternum VI has a broad, low tubercle anterior to it. The frontal grooves are very narrow. The specimen probably bears an incorrect locality label. If not an aberrant *C. planum*, it might belong to an undescribed species from one of the Lesser Antilles, such as Grenada or Saint Lucia, from which no members of the section have yet been described.

THE *ROJASI* SECTION

This section resembles the *guildingii* section in having the intercalary stria abbreviated posteriorly and the intratubercular stria complete. However, the false spurs are absent. The metasternum has the median sulcus well-developed, and the apical tubercle is strongly emarginate. The male has a proximal tooth or angle on the anterior tibia. There are four, or possibly more, species confined to the mountains near the coast of Venezuela, from Falcon State eastward.

Phylogeny.— Unfortunately two of the species, *C. pala* and *C. excavatum* are known only from the females. They show distinctive modifications of Sternum VI. This character suggests that they are sister species. Non-sexual characters, however, suggest that *C. pala* is closest to *C. rojasi* and *C. excavatum*, to *C. bechyneorum*. As noted under "variation", there are possible additional species in this section. An analysis of phylogeny must wait until more material is collected.

Clinidium (sensu stricto) rojasi Chevrolat 1873a (Figs. 179, 184, 185, 186)

Clinidium rojasi Chevrolat 1873a: 211-215.

Clinidium (sensu stricto) rojasi (Chevrolat) Bell and Bell 1978.

Type Material.— We have been unable to study the types of this species. According to the original description, there were two specimens, one collected by Rojas, the other by Salle. Both were labelled simply "Venezuela". Vulcano and Pereira (1975b) studied the types, borrowed from NMW. According to them, both syntypes are female. We studied a female example, labelled: "type, Colonia Tovar, E. Simon, III-88, exemplaire typique" (MNHN). This species is not an authentic type, as it was not listed in the original description, and was collected long after the publication of the name. Thus it is not quite certain which member of the section was really described by Chevrolat. We follow Vulcano and Pereira (1975b) in assigning it to this species, as their illustrations of the male legs show acute calcars and a sharp proximal tooth. The Simon specimen also belongs to this species, as shown by the pollinose frontal space and the absence of setae on the

parasutural stria.

Clinidium simplex Chevrolat 1873b: 378 is difficult to interpret. We have studied a specimen labelled: "Dr. Moritz, 1858, Venezuela, *Clinidium simplex*" (NMW). This was lent to us as the type, but is not labelled as such, and is from the wrong locality. The type locality in the original description is given as "Nova-Grenata". The Vienna specimen is a male *C. rojasi*. However, Vulcano and Pereira (1975b) describe and illustrate a different species under this name, and state that the description is based on a specimen labelled as a type and as from Nova Grenata. It appears to belong to the *rojasi* section, and has the emarginate apical tubercle typical of that section. According to the figure, it is longer and more slender than *C. rojasi*, with the head more narrowed behind. Thus it may represent an additional species in the section. This may also not be the real type, as it differs from the original description in an important feature, in not having double marginal grooves on the pronotum. No South American species of *Clinidium* known to us has double marginal grooves, a feature found in most species of subgenera *Arctoclinidium* and *Mexiclinidium*. At the present time we cannot interpret the name *C. simplex* with any certainty.

Description.— Length 4.7–5.8 mm. Antennal stylet acuminate, elongate, 0.3 of length of Segment XI; latter elongate; tufts of minor setae on Segments V–X; basal setae present on Segments VII–X or VIII–X; Segments I–VIII with pollinose subapical rings; head scarcely longer than wide; base rather broad; margin oblique posterior to eye; frontal grooves deep, narrow, pollinose; median lobe short, broad, triangular, tip even with anterior part of eye; frontal space rather narrow, completely pollinose; medial margins of temporal lobe oblique, slightly divergent posteriorly; posterior, posteromedial margins of temporal lobe bordered by pilosity; orbital groove complete; eye narrow, crescentic, heavily pigmented in most specimens; most specimens with three temporal setae, one midorbital, one postorbital, one posttemporal, one or two of these missing in some specimens; two pairs of postlabial setae.

Pronotum elongate; length/greatest width 1.59; lateral margins curved; apex strongly narrowed; base moderately narrowed; apex truncate, base rounded; median groove nearly linear, expanded at anterior median pit, latter about 0.1 of width of pronotum at apex; basal 0.2 of median groove very shallow, narrow; pollinosity of median groove connected to transverse band at base of pronotum; latter occupying about 0.3 of width of base; basal impressions small, triangular, closed posteriorly; discal striae slightly curved, extending to middle of length of pronotum; marginal groove visible in dorsal view; angular seta anterior, medial to hind angle; nine to 12 marginal setae; discal, precoxal setae absent; anterior part of sternopleural groove absent, posterior part barely indicated.

Elytra short, relatively broad; striae impressed, pollinose, indistinctly punctate; intercalary stria abbreviated posteriorly; apical tubercles inflated, strongly emarginate (Fig. 185); sutural stria with complete row of four to six setae; parasutural stria without setae; intercalary stria with complete row of nine to 11 setae; intratubercular stria with two setae near base, two near apex; marginal stria with complete row of 11–14 setae; anterior medial angle of Interval III with one seta in prominent pollinose pit; apical tubercle with three to six setae in prominent punctures; metasternum with complete median sulcus; in both sexes transverse sulci of abdominal Sterna III–IV entire, those of V and VI interrupted in midline, submarginal groove of Segment VI well separated from transverse sulci, deeply U-shaped in female (Fig. 186), transverse in male; Sternum VI evenly convex in both sexes, with one pair of setae; female with lateral pit in Sternum IV; false spur absent; male without ventral tooth on anterior femur, but with broad, obtuse proximal tooth on anterior tibia (Fig. 184); calcars acute, small.

The acute calcars of the male and the unmodified Sternum VI of the female separate this species from other members of the section.

Range.— Andes of northern Venezuela, from Falcon State (Cerro Galicia) on the west to Aragua State (Tiara) on the east. We have studied the following specimens: one male, one female, labelled: "Caracas, Silla" (MNHB); four males, four females labelled: "Cero Galicia, Venezuela, Falcon, 1500 m., 22-XI-1971, J. & B. Bechyne leg." (VEN); one male, labelled: "Colonia Tovar, capacha bajo, Venezuela, Aragua, 24-IX-1968, en corteza de guamo" (VEN); one female, labelled: "Colonia Tovar, E. Simon, III-88, exemplaire typique" (MNHN); one female, labelled: "Venezuela, Aragua, Tiara, 16-VI-1970, J. & B. Bechyne leg." (VEN); one male, labelled: "Venez., Fry Colln. 1905, 100, 18628." (BMNH). According to the ledger of the Fry Collection in the British Museum, this last specimen was collected at Caracas.

Variation.— An additional female specimen from Tiara has the posterior 0.5 of Sternum VI shallowly impressed and the transverse sulci of Sterna II–VI interrupted at the midline. This specimen might represent an extreme variant of *C. rojasi*, but could also belong to a different species. It was collected with the typical *C. rojasi* female from Tiara referred to above, and bears an identical label.

Clinidium (sensu stricto) bechyneorum new species
(Figs. 180, 187)

Type Material.— HOLOTYPE male, labelled: "Hac. Montero, Montalban, Venezuela, Carabobo, 1300 m., 18-IV-1968, J. & B. Bechyne leg." (VEN). PARATYPES one male, one female, same label as holotype. (VEN)

Description.— Length 5.5-6.0 mm. Antennal stylet acuminate, elongate, 0.3 of length of Segment XI, latter elongate; tufts of minor setae on Segments V-X; basal setae present on Segments VII-X; Segments I-IV with subapical pollinose rings; head as long as broad, base broad, margin not oblique posterior to eye; frontal groove deep, narrow, partly pollinose; median lobe short, broad, triangular, tip opposite anterior part of eye; frontal space rather narrow, anterior 0.5 glabrous, posterior 0.5 pollinose; medial margins of temporal lobes oblique, slightly divergent posteriorly; posterior, posteriomedial margins of temporal lobes bordered by pollinosity; orbital groove complete, wider than in *C. rojasi*; eye narrow, crescentic, longer than in *C. rojasi*; two or three temporal setae; two pairs of postlabial setae.

Pronotum elongate; length/greatest width 1.58; lateral margins curved, slightly sinuate anterior to hind angle; apex strongly narrowed; base moderately narrowed; apex truncate; base rounded; median groove very shallow, narrow; pollinosity of median groove connected to transverse band of pollinosity occupying median 0.3 of base of pronotum; basal impressions small, triangular, closed posteriorly; discal striae slightly curved, extending to middle of length of pronotum; marginal groove fine, visible in dorsal view; angular seta anterior, medial to hind angle; 7-10 marginal setae; discal, precoxal setae absent; sternopleural suture absent.

Elytra short, relatively broad; striae impressed, pollinose, indistinctly punctate; intercalary stria abbreviated posteriorly; apical tubercles inflated, strongly emarginate; sutural stria without setae or with one or two near apex; parasutural stria with two to four setae; intercalary stria with complete row of four or five; intratubercular stria without or with one basal and without or with one apical seta; marginal stria with complete row of eight to 15 setae; apical tubercle with two to five setae in prominent punctures; metasternum with complete median sulcus; in both sexes, transverse sulci of Sternum III, IV entire, those of V, VI interrupted in midline; submarginal sulcus of Sternum VI in both sexes short, scarcely curved (Fig. 187); Sternum VI with one pair of setae; Sternum VI evenly convex, similar to that of male; false spur absent; male without ventral tooth on anterior femur, with broad, obtuse proximal tooth on anterior tibia; calcars obtusely rounded at apices.

The presence of setae in the parasutural stria, the rounded calcars of the male, and the shape of the submarginal sulcus of Sternum VI of the female separate this species from *C. rojasi*. The evenly convex Sternum VI of the female separate it from *C. excavatum*. We dedicate this species to J. & B. Bechyne whose fine series of *Clinidium* have made the Rhysodine fauna of Venezuela the best known of any South American country.

Variation.— A single male specimen, labelled: "Venezuela, Aragua, Rancho Grande, 1400 m., 26-VIII-70, J. & B. Bechyne leg." (VEN) may represent this species. It is in poor condition, with middle and hind legs missing, and with most setae of the head missing. It was probably dead when found. The orbital groove is very narrow and the pollinosity is very reduced at the posterior margin of the temporal lobe, exposing a distinct occipital angle. It is not clear whether this represents a real difference from *C. bechyneorum* or is the result of abrasion after death. The regular arrangement of the pollinosity suggests that the former is more probably. The absence of the middle and hind legs prevents comparison of the calcars with those of *C. bechyneorum*. We suspect that this specimen represents an additional species, but decline to name it until better material is available.

Clinidium (sensu stricto) excavatum new species
(Fig. 188)

Type Material.— HOLOTYPE female, labelled: "Venezuela-Carabobo-Montalban Oeste 1800 mts. 26-VI-1968, C. J. Rosales, A. D. Ascoli" (VEN). PARATYPE one female, same label as holotype. (VEN)

Description.— Length 6.5-6.8 mm. Identical to *C. bechyneorum* in most respects, but larger with more elytral setae, and with Sternum VI strikingly modified. Setae within the ranges given for *C. bechyneorum*, except for intercalary stria, with eight setae and intratubercular without or with one at base and three near apex. Sternum VI with deep concavity in posterior 0.33, evidently representing a greatly enlarged submarginal sulcus; cavity bounded anteriorly by scarp, latter with broad rectangular lobe in midline, bordered on each side by deep, prominent notch (Fig. 188). Male

unknown.

C. pala has a similarly modified sternum, except that the notches are much closer together and are convergent anteriorly.

Clinidium (sensu stricto) pala new species

(Fig. 189)

Type Material.— HOLOTYPE female, labelled: "VEN: ,Edo. Miranda Guatopo Nat. park, 50 km. SE Caracas, 5-6 III, 1971, 400m forest & hum dung" (BSRI). PARATYPE one female, same label as holotype. (BSRI)

Description.— Length 5.0-5.5 mm. Antennal stylet acute, both stylet and Segment XI less elongate than in *C. rojasi*; tufts of minor setae on Segments V-X; basal setae present on Segments VI-X or VII-X; Segments I-VIII ringed with pollinosity; head distinctly longer than wide, longer, narrower, more parallel-sided than in *C. rojasi*; frontal groove deep, narrow, pollinose, median lobe short, rather narrow, triangular, tip opposite anterior margin of eye; frontal space narrow, anterior part scarcely pollinose; medial margins of temporal lobes oblique, slightly divergent posteriorly; posterior, medial margins of temporal lobes bordered by pilosity; orbital groove complete; eye very narrow, crescentic; two temporal setae; two pairs of postlabial setae.

Pronotum elongate; length/greatest width 1.53; lateral margins curved; apex strongly narrowed; base moderately narrowed; apex truncate; base rounded; median groove nearly linear, scarcely expanded at anterior median pit; latter smaller than in *C. rojasi*; basal 0.2 of median groove very narrow, shallow; pollinosity of median groove connected to transverse band at base of pronotum, latter occupying about 0.3 of basal width; basal impressions small, triangular, closed posteriorly; discal striae curved, extending almost to middle of length of pronotum; marginal groove visible in dorsal view; angular seta anterior, medial to hind angle; eight or nine marginal setae; discal, precoxal setae absent; anterior part of sternopleural groove shallow, posterior part deep, incomplete.

Elytra short, relatively broad; striae impressed, pollinose, indistinctly punctate; intercalary stria abbreviated posteriorly; apical tubercles inflated, strongly emarginate; sutural stria with complete row of four or five setae; parasutural without setae; intercalary stria with complete row of six to eight setae; intratubercular stria with one or two setae near base, two near apex; marginal stria with complete row of 12-14 setae; anterior medial angle of Interval III with one seta in prominent pollinose pit; apical tubercle with eight or nine setae in prominent punctures; metasternum with median sulcus; transverse sulcus of abdominal Sternum III entire, those of IV-VI interrupted in midline; tibiae without false spurs; female with lateral pit in Sternum IV, smaller one in Sternum V; female with Sternum VI with submarginal groove greatly expanded, forming deep concavity occupying posterior 0.33 of sternum, limited anteriorly by scarp, latter interrupted by pair of notches which are convergent anteriorly defining narrow, trapezoidal median lobe (Fig. 189); male unknown.

The absence of setae from the parasutural stria link this species to *C. rojasi*. The latter species has a shorter, broader head, and does not have Sternum VI modified in the female. The form of Sternum VI in *C. pala* is similar to that of *C. excavatum* except that the median lobe is much broader and more rectangular in the latter.

THE *CAVICOLLE* GROUP

This group resembles the *gildingii* group in having tufts of minor setae present on Antennal Segments V-X. It differs strongly in having the anterior median pit greatly enlarged. In all species except *C. mathani* the pit contains a prominent median tubercle. False spurs are absent. The form of the anterior median pit is strongly similar to that of *C. dubium*, in the *insigne* group, and the latter species might really be more closely related to the *cavicolle* group than to *C. insigne*.

There are nine species in the *cavicolle* group. They are restricted to southern Central America and northwestern South America, from Costa Rica to Ecuador, eastern Colombia, and the western part of Amazonas State, Brazil.

Phylogeny.— Phylogenetic relationships within this group are not clear. Of the nine species, both sexes are known in only three. Our tentative conclusions about relationships are reflected in the key. This arrangement might be altered substantially when both sexes of all species have been studied. The most distinctive species is *C. mathani*, which has the intercalary stria

abbreviated and lacks the tubercle in the anterior median pit. Both of these features, however, might be derived characters, and *C. mathani* might not be the sister group to the remaining species. Similarly, *C. humile*, the only species to lack a median sulcus of the metasternum, might have lost the sulcus secondarily, and might be close to *C. cavicolle*. We placed *C. centrale* and *C. validum* together because of the similar arrangement of temporal setae and the presence of pollinosity along the notopleural suture. However, *C. centrale* resembles *C. curvatum*, *C. humile* and *C. cavicolle* in having a round anterior median pit, while *C. validum* has a pit which combines a truncate anterior margin, as in *C. crater*, and sinuate margins, as in *C. foveolatum*. We provisionally attribute similarities in the anterior median pit to convergent evolution. It is possible that we are wrong, and that the similarities in chaetotaxy and pollinosity between *C. centrale* and *C. validum* are themselves the result of convergence. Further conclusions will have to await the collection of more specimens of this excessively rare group, of which we have studied only about 15 specimens.

Clinidium (sensu stricto) mathani Grouvelle 1903
(Figs. 182, 192, 193)

Clinidium mathani Grouvelle 1903: 131.

Clinidium (sensu stricto) mathani (Grouvelle) Bell and Bell 1978.

Type Material.— HOLOTYPE male, labelled: "St. Paulo d'Olivencia, Amazonas, M. de Mathan" (MNHN). The locality is on the upper Amazon in Brazil, close to the border with Peru and Colombia.

Description.— Length 6.3 mm. Antennal stylet conical, very large, about 0.4 of length of Segment XI, apex blunt; tufts of minor setae present on Segments V-X; basal setae on Segments VII-X; Segment I with subapical pollinosity; head slightly longer than wide; clypeal setae present, frontal grooves shallow, effaced anteriorly; median lobe narrow, tip opposite anterior 0.3 of eye; frontal space narrow; medial margins of temporal lobe oblique; convergent posteriorly, nearly contiguous at distinct medial angles; temporal lobe broadly bordered by pilosity posteriorly; eye crescentic, relatively broad, about 0.5 of length of temporal lobe; orbital groove complete; one temporal seta, in orbital groove behind eye; two pairs of postlabial setae.

Pronotum elongate; length/greatest width 1.50; pronotum widest slightly anterior to middle; lateral margins curved; base moderately narrowed, curved; apex strongly narrowed, truncate; median groove dilated, basal 0.33 shallow but broad; middle 0.33 deep, broad, margins parallel, apical 0.33 occupied by anterior median pit, latter elliptical, without tubercle, 0.25 of width of pronotum; basal impression small, triangular, open posteriorly; discal striae elongate, curved, 0.60 of length of pronotum; marginal groove visible in dorsal view; angular seta present; three or four marginal setae; notopleural suture not pollinose; sternopleural groove broadly interrupted.

Elytra moderately elongate; striae deep, pollinose, very coarsely punctate; intercalary stria abbreviated posteriorly (Fig. 193); intratubercular stria strongly dilated near apex; preapical tubercle strongly inflated, truncate at apex, tubercles separated by combined widths of sutural intervals; sutural stria without setae; parasutural stria with complete row of four setae; intercalary with complete row of six setae; intratubercular stria with one seta near apex; marginal stria with five setae in apical 0.2; preapical tubercle with three or four setae; apical tubercle without setae; metasternum with median sulcus; abdominal Sterna III-VI each with transverse sulci complete, not interrupted in midline; submarginal sulcus of Sternum VI broad, curved, not joined to transverse sulcus (Fig. 192); male without ventral tooth on anterior femur, without proximal tooth on anterior tibia; middle calcar small, acute; hind calcar small, narrowly triangular, apex obtuse. Female unknown.

This species is recognized by the abbreviated intercalary stria and by the elongate elliptical anterior median pit, without a median tubercle.

Range.— Amazon Basin. Vulcano and Pereira (1975b) record it from Cerro de Nairo, Amapá Territory.

Clinidium (sensu stricto) humile new species
(Figs. 181, 190)

Clinidium cavicolle Chevrolat 1873b: 388 (*pars*)

Type Material.— HOLOTYPE male, labelled: "*cavicolle*, New Granada, Chev. type" (NMW). This specimen matches one discussed in the original description of *C. cavicolle* Chevrolat, as a possible representative of "the other sex" of *C. cavicolle*. It is a male, while the lectotype of *C. cavicolle* is a female, but the two are not conspecific.

Description.— Length 6.8 mm. Antennal stylet conical, relatively small, about 0.15 of length of Segment XI; tufts of minor setae on Segments V-X; basal setae sparse on Segments IX, X; Segments I-IX with subapical pollinose rings; head short, broad, scarcely longer than wide, width behind eyes nearly equal to width across eyes; clypeal setae present; frontal grooves deep, entire; median lobe narrow, tip opposite anterior 0.33 of eye; frontal space narrow, sides parallel; medial margin of temporal lobe narrowly pilose, posterior margin broadly pilose; eye crescentic, narrow; orbital groove complete, broad; three temporal setae all posterior to eye; three or four pairs of postlabial setae.

Pronotum rather short, length/greatest width 1.39; pronotum widest slightly posterior to middle, lateral margins strongly curved; base moderately narrowed, curved; apex strongly narrowed, truncate; median groove dilated; gradually broader anteriorly to anterior medial pit; latter rounded anteriorly, sides evenly curved, with large round median tubercle; greatest width 0.33 of that of pronotum; basal impressions small, triangular, open posteriorly; discal striae long, curved, 0.6 of length of pronotum; marginal groove visible in dorsal view; angular seta present; five to seven marginal setae; notopleural suture not pollinose; sternopleural groove absent.

Elytra moderately elongate; striae deep, pollinose, punctate; intercalary stria slightly dilated posteriorly; preapical tubercles scarcely inflated, rounded at apex, widely separated; sutural stria without setae; parasutural stria with one seta at base; intercalary stria with three setae in anterior 0.3; intratubercular stria with one seta at base; marginal stria with four setae in anterior 0.25, four setae in posterior 0.25; preapical tubercle without setae; metasternum without median sulcus; abdominal Sterna III-V with transverse sulci rather narrowly interrupted in midline; transverse sulcus of Sternum VI reduced to small oval pit, widely separated from submarginal sulcus (Fig. 190); Sternum VI with two pairs of setae; femora with dorsal pollinosity; male with large ventral tooth on anterior femur, without proximal tooth on anterior tibia; middle calcar small, triangular, acute; hind calcar slightly larger, subtriangular, obtuse. Female unknown.

This species is the only member of the group in which the metasternum lacks a median sulcus. It differs from *C. cavicolle*, in having a shorter, broader head; dorsal sides of femora pollinose, and Sternum VI with submarginal sulcus separate from transverse sulci. The last two characters might be secondary sexual differences, rather than species differences, since *C. cavicolle* is represented only by females and *C. humile* only by males.

Clinidium (sensu stricto) curvatum new species
(Figs. 194, 203)

Type Material.— HOLOTYPE male, labelled: "Oroque, Colombia, Santander del Norte, 10-VI-1965, J. & B. Bechyne leg." (VEN). PARATYPES one broken female, same label as holotype (VEN).

Description.— Length 6.2 mm. Antennal stylet elongate, acute, 0.4 of length of Segment XI; tufts of minor setae on Segments V-X; basal setae absent; Segment I with subapical pollinose ring; head slightly longer than wide; frontal grooves narrow, deep; clypeal setae present; median lobe short, broad, triangular, tip anterior to anterior margin of eye; frontal space very narrow, sides parallel; medial margin narrowly pilose; posterior margin broadly pilose; eye crescentic, narrow; orbital groove complete; two temporal setae, one medial to posterior margin of eye, other posteriomedial to it; two pairs of postlabial setae.

Pronotum moderately elongate, length/greatest width 1.52; widest slightly behind middle, lateral margins strongly curved; base moderately narrow, curved; apex strongly narrowed, truncate; median groove narrow, almost linear except at anterior median pit; latter 0.33 of length of pronotum, about 0.3 of width of pronotum, margins divergent nearly to apex, there strongly narrowed, with very large round median tubercle; basal impressions small, rounded, open posteriorly; discal striae long, curved, about 0.45 of length of pronotum; marginal groove fine, visible in dorsal view; angular seta present, medial to hind angle; five or six marginal setae; notopleural suture not pollinose; sternopleural groove absent.

Elytra rather short; striae deep, pollinose, punctate; intercalary stria not abbreviated posteriorly; intratubercular stria slightly dilated posteriorly; preapical tubercles moderately dilated posteriorly, widely separated; sutural striae without setae; parasutural stria with one seta at base; intercalary stria with complete row of six setae; intratubercular stria with one seta at base, three near apex; marginal stria with complete row of about 15 setae; apical tubercle with one or two setae; metasternum with median sulcus; abdominal Sterna III-V in both sexes with transverse sulci broadly interrupted in middle; in female, large lateral pit on Sternum IV, smaller on Sternum III; Sternum VI of male with short, slightly oblique transverse sulci, narrowly separated from submarginal sulcus, three or four pairs of setae; female with each transverse sulcus of Sternum VI broken into two pits (Fig. 203); two pairs of setae; in both sexes, submarginal sulcus curved, extending nearly to transverse sulci; middle, hind tibiae each with only one spur, femora not pollinose dorsally; male with ventral tooth on anterior femur, without proximal tooth on anterior tibia; middle calcar triangular, apex obtuse; hind calcar subtriangular, apex narrowly truncate; ventral margin with minute tooth anterior to spur.

This species resembles *C. cavicolle* in general appearance, but differs in having shorter discal striae, distinct transverse sulci on Sternum VI and a narrower anterior median pit with margins oblique and nearly straight.

Clinidium (sensu stricto) foveolatum Grouvelle
(Figs. 195, 204)

Clinidium foveolatum Grouvelle 1903: 130-131.

Clinidium (sensu stricto) foveolatum (Grouvelle) Bell and Bell 1978.

Type Material.— HOLOTYPE female, labelled: "Ecuador, Siemiradski 1882-1883, *Clinidium foveolatum* Grouvelle, type" (MNHN).

Description.— Length 6.7 mm. Antennal stylet elongate, acute, 0.5 of length of Segment XI; tufts of minor setae present on Segments V-X; basal setae present on Segments VI-X; subapical pollinose rings on Segments I-IX; head as long as wide; clypeal setae absent; frontal grooves deep, rather broad; median lobe narrow, triangular, tip opposite middle of eye; frontal space moderately wide, margins slightly convergent posteriorly; medial margin narrowly bordered with pilosity; posterior margin widely bordered by pilosity; eye crescentic, rather short; orbital groove complete, rather broad; three temporal setae, in orbital groove, one opposite posterior part of eye, one near occiput, one between them.

Pronotum oval, rather short; length/greatest width 1.36; widest near middle, lateral margins strongly curved; base moderately narrowed, curved; apex very narrow, truncate; median groove with basal 0.5 moderately narrow, sides parallel; apical 0.5 strongly dilated, margin sinuate, curved medially opposite tubercle of anterior median pit, dilated, rounded anterior to constriction, tubercle transverse, oval; basal impression very small, triangular, open posteriorly; discal striae short, 0.2 of length of pronotum; marginal groove visible in dorsal view; angular seta present; six or seven marginal setae; sternopleural groove absent except near anterior margin.

Elytra elongate; striae deep, pollinose, indistinctly punctate; intercalary stria not abbreviated posteriorly; intratubercular stria scarcely dilated near apex; preapical tubercles moderately dilated, widely separated posteriorly; sutural stria without setae; parasutural stria with one seta near middle, one near apex; intercalary stria with complete row of seven setae; intratubercular stria with one seta at base, one near apex; marginal stria with complete row of about 11 setae; apical tubercle with three or four setae; metasternum with median sulcus; transverse sulcus of abdominal Sternum III not interrupted; those of IV-VI narrowly interrupted at midline; that of Sternum VI separated from submarginal sulcus (Fig. 204); all transverse sulci coarsely punctate; female with shallow lateral pit on Sternum IV; middle, hind tibiae with two small spurs; male unknown.

The very short discal striae separate this species from all others except for *C. centrale*. The latter species has the margin of the anterior median pit rounded. The shape of the anterior median pit in *C. foveolatum* resembles that of *C. spatulatum*, but the latter species has a well developed discal stria and a much smaller antennal stylet.

Clinidium (sensu stricto) cavicolle Chevrolat 1873b
(Figs. 183, 191)

Clinidium cavicolle Chevrolat 1873b: 388.

Clinidium (sensu stricto) cavicolle (Chevrolat) Bell and Bell 1978.

Type Material.— LECTOTYPE, here designated, female, labelled: "*C. cavicolle*, Colombia, Steinheil, Ocaña (Landolt)", with red "typus" label (NMW). There is doubt as to whether this is the specimen described by Chevrolat, as he gives the locality as "Nova-Grenata, Bogoto". The latter is presumably a misspelling of "Bogota". Nevertheless, this specimen fits the original description better than the other syntype, described above as *C. humile* new species. The latter is the specimen discussed by Chevrolat as "probably another sex" of *C. cavicolle*.

Description.— Length 6.0-7.0 mm. Antennal stylet conical, rather small, about 0.2 of length of Segment XI; Segment XI somewhat compressed; tufts of minor setae on Segments V-X; basal setae present on Segments IX, X; Segments I-X with subapical pollinose rings; head slightly longer than in *C. humile*, with lateral margins more parallel, base more abruptly truncate; clypeal setae present; frontal grooves deep, entire; median lobe narrow, short, tip anterior to eye; frontal space narrow, sides parallel; medial margin of temporal lobe narrowly pilose; posterior margin broadly pilose; eye crescentic, narrow, rather short; orbital groove complete, broad; two temporal setae, one near posterior margin of eye, the other near occiput; one or two pairs of postlabial setae.

Pronotum rather short, oval; length/greatest width 1.39; pronotum widest near middle, margins strongly curved; base narrow, rounded; apex narrowly truncate; median groove dilated, margins parallel except in apical 0.25, opposite anterior median pit; median groove pollinose near base, otherwise with margins pollinose, middle glabrous; anterior median pit

rounded, about 0.33 of width of pronotum, lateral margins with long pilosity; median tubercle round; basal impression small, triangular, open posteriorly; discal striae long, 0.6 of length of pronotum, strongly curved; marginal groove visible in dorsal view; angular seta present, medial, anterior to hind angle; eight or nine marginal setae; notopleural suture not pollinose; sternopleural groove incomplete.

Elytra moderately elongate; striae deep, broad, pollinose, punctate; intervals narrow, subcostate; intercalary stria not abbreviated posteriorly; intratubercular stria slightly dilated posteriorly; preapical tubercle slightly dilated; sutural stria without setae; parasutural stria with one seta at base, two near apex; intercalary stria with seven setae in complete row; intratubercular stria with one seta at base, three or four near apex; marginal stria with complete row of about 15 setae; apical tubercle with two or three setae; metasternum with complete median sulcus; abdominal Sterna III-V broadly interrupted in midline; Sternum VI without transverse sulci, with submarginal sulcus long, curved, reaching nearly to anterior margin (Fig. 191); one or two pairs of setae on Sternum VI; female with large lateral pit in Sternum III, smaller one on Sternum IV; middle, hind tibiae each with one spur; femora not pollinose on dorsal surface. Male unknown.

The large, oval anterior median pit and the long, curved discal striae make this species resemble *C. humile*. The latter species, however, lacks the median sulcus on the metasternum, has a broader head, and pollinosity on the dorsal surface of the femora.

Range.— Colombia. Hincks (1950) also lists it from Brazil, but without a definite locality. We have been unable to find the source of this record. In addition to the lectotype, we have seen two females, labelled: "Mesa Rica, Colombia, Santander del Norte, 2500 m., 2-VI-1965, J. & B. Bechyne, leg." (VEN).

Clinidium (sensu stricto) crater new species

(Figs. 196, 205)

Type Material.— HOLOTYPE female, labelled: "PANAMA: Cerro Jefe, Azul Ridge, 9° 12' N. 79° 21' W, 700-750 m., cloud for., 20 May, 72, T. L., L. J. Erwin coll. Exped. #10, notebook #1, loose bark, log ADP01472" (NMNH). PARATYPES two females, labelled: "PANAMA, Province of Panama, Cerro Jefe, 1000 m., 21-V-1977, coll. Lloyd Davis, under dead bark, fallen hardwood" (UVM).

Description.— Length 5.9-6.9 mm. Antennal stylet near conical, small, about 0.2 of length of Segment XI, slightly curved; Segment XI slightly compressed; tufts of minor setae on Segments V-X; basal setae on Segments VI-X; subapical pollinose rings on Segments I-X; head slightly longer than wide; clypeal setae present; frontal grooves deep, entire; median lobe short, narrow, tip anterior to eye; frontal space narrow, sides slightly divergent posteriorly; medial margin of temporal lobe narrowly pilose; posterior margin very broadly pilose, to level of posterior margin of eye; eye narrow, crescentic, rather short; orbital groove complete, rather broad; two temporal setae, one near posterior margin of eye, other in middle of pollinosity near occiput; two pairs of postlabial setae.

Pronotum rather short, oval, length/greatest width 1.41; pronotum widest near middle, margins strongly curved, base narrow, rounded; apex narrowly truncate; median groove broadened from base to apex; basal 0.2 narrow, parallel, margins anterior to there oblique, divergent; anterior median pit over 0.5 of width of pronotum, margins sinuate opposite tubercle, latter rounded; anterior margin of pit transverse; sides of anterior median pit long, pilose; basal impression small, triangular, open posteriorly; discal striae long, over 0.66 of length of pronotum, curved; marginal groove visible in dorsal view; angular seta present, anterior, medial to hind angle; about nine marginal setae; notopleural suture not pollinose; sternopleural groove incomplete.

Elytra moderately elongate; striae deep, broad, pollinose, truncate; intervals narrow, subcostate; intercalary stria not abbreviated posteriorly; intratubercular stria slightly dilated posteriorly; preapical tubercles slightly inflated; sutural stria without setae or with one or two setae near apex; parasutural stria with complete row of eight setae; intercalary stria with complete row of eight setae; intratubercular stria with three setae near apex; marginal stria with about 15 setae; apical tubercle with two or three setae; metasternum with median sulcus; abdominal Sternum III with transverse sulcus entire; sulci of Sterna IV, V narrowly interrupted in midline; Sterna III, IV with shallow lateral pits in female; Sternum VI without transverse sulci, submarginal sulcus shorter than in *C. cavicolle* restricted to posterior 0.5 of sternum (Fig. 205); femora with dorsal surface pollinose; one spur on each middle, hind tibia. Male unknown.

The shape of the median groove of the pronotum in this species is closest to that of *C. validum*. In the latter species, however, the anterior median pit is larger, the notopleural suture is pollinose, and there are two tibial spurs.

Clinidium (sensu stricto) centrale Grouvelle 1903
(Figs. 197, 200)

Clinidium centrale Grouvelle 1903: 133-134.

Clinidium (sensu stricto) centrale (Grouvelle) Bell and Bell 1978.

Type Material.— HOLOTYPE male, labelled: "Costa Rica, *C. centrale* Grouv., type" (MNHN). Two additional specimens, labelled as types (MNHN), must have been so marked by accident, as they bear collecting dates later than 1903.

Description.— Length 6.0-7.4 mm. Antennal stylet slender, small, about 0.2 of length of Segment XI; tufts of minor setae on Segments V-X; basal setae on Segments VII-X; subapical pollinose rings on Segments I-X; head scarcely longer than wide, clypeal setae present; frontal grooves deep, entire, pollinose; median lobe short, broad, tip obtuse, opposite anterior margin of eye; frontal space very narrow, sides parallel; medial margin of temporal lobe narrowly pollinose; posterior margin very broadly pollinose, to level of posterior margin of eye; base of temporal lobe nearly transverse, abruptly curved to lateral margin, latter nearly longitudinal behind eye; eye narrow, crescentic, rather short; orbital groove complete; temporal lobe with one or two setae variously placed in large isolated pollinose punctures medial to eye, three temporal setae in transverse row in pilosity of posterior margin; three pairs of postlabial setae.

Pronotum rather elongate, length/greatest width 1.58; widest near middle; margins strongly curved, base narrow, curved; apex strongly narrowed, truncate; median groove moderately dilate, parallel-sided in basal 0.25; anteriorly, evenly broadened to anterior medial pit; nearly evenly rounded anterior to pit; pit 0.33 as wide as pronotum; tubercle rounded; sides of anterior median pit rather short, pilose; basal impression triangular, open posteriorly; discal striole short, about equal in length to basal impression; length of impression plus striole about 0.33 of length of pronotum; marginal groove visible in dorsal view; 1 angular seta, 8-11 marginal setae; notopleural suture pollinose (continuous in some specimens, interrupted anterior to middle in others); sternopleural groove absent.

Elytra rather elongate; striae impressed, pollinose, punctate; intercalary stria not abbreviated at apex; apex of intratubercular stria slightly dilate; preapical tubercle slightly inflated; sutural stria without setae; parasutural stria with complete row of six or seven setae; intercalary stria with complete row of nine or 10 setae; intratubercular stria with one seta at base, two near base; marginal stria with complete row of about 15 setae; preapical tubercle with one seta in prominent puncture; apical tubercle with two or three setae; metasternum with median sulcus; transverse sulci of Sterna III-VI entire in male; in female, sulcus of Sternum V narrowly interrupted, others entire; Sternum VI with submarginal sulcus rather broadly separated from transverse sulcus (Fig. 200); Sternum VI with two or three pairs of setae; female with deep lateral pit on Sternum IV; dorsal surface of femora with pollinosity; middle, hind tibiae each with two equal spurs; anterior femur of male with prominent ventral carina; anterior tibia of male with proximal tooth; calcars acute, triangular.

The pollinose notopleural suture and isolated setose punctures on the temporal lobe separate this species from all species except *C. validum*, which has a much larger, sinuate anterior median pit. The discal strioles of the pronotum are only slightly shorter than those of *C. curvatum* but the latter species has a smaller anterior pit and only one spur on each tibia.

Range.— Costa Rica. We have seen the following specimens with specific locality data: one female, labelled: "Costa Rica, Coté de Tablazo, 1904, coll. P. Biolley" (MNHN); one specimen, sex not recorded, labelled: "Sta. Maria de Dota, 1600 m., 1-1907" (MNHN) (The two preceding are incorrectly labelled as types.); two males, four females, labelled: "Coronado, Costa Rica, VI-27-1967, E. B. Fagan" (FLA); one female, same locality as previous group but dated V-30-1967, elev. 5500 ft. (FLA). 20 males, 9 females, labelled: "Costa Rica: Cartago Prov., 5 km. S. El Empalme, VII-14-73, J. Doyen & P. A. Opler Coll." (UCB).

Clinidium (sensu stricto) validum Grouvelle 1903
(Figs. 199, 202)

Clinidium validum Grouvelle 1903: 133.

Clinidium (sensu stricto) validum (Grouvelle) Bell and Bell 1978.

Type Material.— HOLOTYPE male, labelled: "Teffé (Ega, Amazonas, M. de Mathan 3^{me} trimestre 1878, *C. validum* Grouv." (MNHN). The locality is in Brazil, several hundred kilometers west of Manaus.

Description.— Length 5.8-6.4 mm. Antennal stylet slender, small, about 0.2 of length of Segment XI; tufts of minor setae on Segments V-X; basal setae on Segments VI-X or VII-X; subapical pollinose rings on Segments I-X; head slightly longer than wide; clypeal setae present; frontal grooves deep, entire, median lobe short, narrow, tip opposite anterior margin of eye; frontal space moderately narrow, sides slightly divergent posteriorly; medial margin of temporal lobe narrowly pilose; posterior margin very broadly pollinose to level of posterior margin of eye; eye crescentic, rather broad of subgenus; orbital groove complete; one or two temporal setae medial to eye, in large punctures surrounded by pollinose spots, latter in partial contact with pilosity of posterior margin; three or four smaller setae among long pilosity of

occiput; three pairs of postlabial setae.

Pronotum rather elongate, length/greatest width 1.55, oval, widest near middle, sides curved; apex truncate, less narrowed than in other members of group; base moderately narrowed, rounded; median groove dilated, posterior 0.5 parallel-sided except for slight dilation at posterior median pit; margins anterior to middle divergent to anterior median pit; latter very large, margins oblique, divergent to level of tubercle; side suddenly broadened anterior to tubercle, apex broadly rounded; margins of anterior median pit very long pilose; pit over 0.66 of width of pronotum opposite it; basal impressions small, triangular, open posteriorly; discal striole very long, curved, 0.67 of length of pronotum; marginal groove visible in dorsal view; angular seta present; eight to 10 marginal setae; notopleural suture pollinose; sternopleural groove incomplete.

Elytra rather elongate; striae impressed, pollinose, punctate; intercalary stria not abbreviated posteriorly; intratubercular stria strongly dilated at apex; preapical tubercles strongly inflated, apex rounded, nearly contiguous; sutural stria without setae; parasutural stria with complete row of six or seven setae; intercalary stria with complete row of 10 setae; intratubercular stria with one seta at base, three near apex; marginal stria with about 20 setae; preapical tubercle with two setae; metasternum sulcate; transverse sulci of abdominal Sterna III-VI in male, very narrowly interrupted in female; submarginal sulcus of Sternum VI rather broadly separated from transverse sulcus (Fig. 202); Sternum VI with two to four pairs of setae; female with lateral pit on Sternum IV; dorsal surfaces of femora pollinose; middle, hind tibiae with two equal spurs; male with anterior femur without ventral tooth or carina; male with prominent proximal tooth on anterior tibia; calcars small, triangular, acute.

The greatly enlarged anterior median pit of this species resembles only that of *C. crater* in shape. The latter species has the pit smaller, and the preapical tubercle of the elytron much less prominent. In addition, the middle and hind tibiae have only one spur.

Range.— Widespread in the Amazon Basin. In addition to the type, we have seen one male, three females from Ega (BMNH), and one specimen, sex not recorded, from Para (MNH). Vulcano and Pereira (1975b) record it also from Serro do Navio, Amapá Territory.

Clinidium (sensu stricto) spatulatum new species

(Figs. 198, 201)

Type Material.— HOLOTYPE female, labelled: "PANAMA:Colon Prov. Santa Rita Ridge, 300 m, 10-11, VI-77, H.&A. Howden:" (BSRI).

Description.— Length 6.6 mm. Antennal stylet slender, small, about 0.2 of length of Segment XI; tufts of minor setae on Segments V-X; basal setae on Segments VII-X; subapical pollinose rings on Segments I-X; head slightly longer than wide; clypeal setae present; frontal grooves deep, entire, median lobe short, narrow, tip opposite anterior margin of eye; frontal space moderately narrow, sides slightly divergent posteriorly; medial margin of temporal lobe narrowly pillinose; posterior margin very broadly pollinose to level of posterior margin of eye; eye crescentic in lateral view, narrower than in *C. validum*; orbital groove complete; four temporal setae as follows: one pair at posterior end of eye; one pair near middle of temporal lobe opposite posterior margin of eye, in partially isolated tuft of pollinosity; two pairs posterior to eye; two pairs of postlabial setae.

Pronotum rather elongate, length/greatest width 1.43, oval, widest near middle, sides curved; apex truncate, less narrowed than in other species (except for *C. validum*); base moderately narrowed, rounded; median groove dilated, posterior 0.5 nearly parallel-sided except for slight dilation opposite posterior median pit; apical 0.5 strongly dilated, margin sinuate, curved medially opposite tubercle of anterior median pit, strongly dilated both anterior and posterior to constriction; tubercle nearly round, slightly transverse; basal impression small, open posteriorly; discal striole straight, about 0.45 of length of pronotum; marginal stria visible in dorsal view; angular seta present; seven or eight marginal setae; notopleural suture inconspicuously pollinose; sternopleural groove absent except for small pollinose spot near anterior margin of prothorax.

Elytra rather elongate; striae impressed, pollinose, punctate; all striae complete; intratubercular stria dilated at apex; preapical tubercle strongly inflated, apex rounded, well separated from opposite tubercle, medial margin appearing "scalloped" by depressed pilose areas around setal punctures; sutural stria without setae; parasutural stria with complete row of six setae; intercalary stria with complete row of 12 setae; intratubercular with one seta at base, and three near apex; marginal stria with complete row of about 20 setae; preapical tubercle with two setae; metasternum sulcate; transverse sulci of abdominal Sterna III-VI entire in female; submarginal sulcus of Sternum VI broadly separated from transverse sulcus; Sternum VI with two pairs of setae (Fig. 201); female with minute lateral pit on Sternum IV; dorsal surfaces of femora pollinose; middle, hind tibiae with two equal spurs; male unknown.

This species resembles *C. foveolatum* in having a very large anterior median pit with a strong constriction opposite the tubercle. The latter species differs in the virtual absence of the discal strioles and in having a much larger antennal stylet. *C. curvatum* has discal strioles of about the same length, as *C. spatulatum* but the strioles are curved, the anterior median pit is

smaller with the constriction merely suggested, and the stylet is much larger. *C. validum* has a large anterior median pit, but with the margin oblique posteriorly, not strongly sinuate, while the discal striole is longer and the sternopleural groove is better developed.

THE BECCARII GROUP

These four species are unique in the tribe in entirely lacking minor setae on Segments IV-X. As in all other Rhysodini, however, there are scattered minor setae on Segment XI. The compound eye is either constricted at its middle or else entirely divided into two structures resembling ocelli. The male has the midline of the anterior abdominal sterna modified with a sulcus or paired tubercles. The antennal stylet is elongate and compressed, with the tip obliquely truncate.

The range of the group is in doubt. *C. moldenkei* is the only species collected independently by more than one collector. It is certainly from Costa Rica. There is no reason to doubt that the single specimen of *C. sulcigaster* is from nearby Guatemala, as it was collected recently and has exact data. The two remaining species are supposedly from the southwestern Pacific, *C. argus*, from Negros, Philippine Islands, and *C. beccarii* from New Guinea. The holotype of *C. beccarii* has exact locality data, and Beccari was a notably careful collector. According to Dr. Poggi (*in litt.*) not one of his specimens has previously been shown to be mislabelled. If it were not for this, we would be almost certain that the specimen is mislabelled, as the distribution is totally unexpected within a group of closely related species. Moreover, the entire subgenus is otherwise strictly neotropical. It is still possible that Grouvelle or some other person inadvertently interchanged labels between this and some other specimen. One should be open-minded about the range of this group until more specimens of *C. beccarii* or *C. argus* come to light, either from their supposed localities, or from somewhere in Central America.

Phylogeny.— The group clearly consists of two pairs of closely related species. In *C. moldenkei* and *C. sulcigaster*, the eye is bilobed, the median groove of the pronotum is much narrower than the anterior median pit, and the anterior part of the sternopleural groove is absent. In *C. beccarii* and *C. argus* the eye is completely divided, the median groove is almost as wide as the anterior median pit, and the anterior part of the sternopleural groove is present.

Clinidium (sensu stricto) moldenkei new species (Figs. 206, 210, 211, 212)

Type Material.— HOLOTYPE male, labelled: "COSTA RICA, Rincon de Osa VII-15-66, A. R. Moldenke, borrowed ex G. E. Ball ADP 38023" (NMNH). PARATYPES three males, two females, labelled: "Rincon de Osa, Puntarenas, Costa Rica, 100 m., 3-X-1969, Halffter & Reyes" (MZSP).

Description.— Length 6.8-7.8 mm. Stylet elongate, 0.4 of length of Segment XI, compressed, apex obliquely truncate; minor setae absent except for Segment XI, basal setae absent; Segments I-X each with subapical pollinose rings; median lobe small, shield-shaped, frontal grooves broad, pollinose; temporal, antennal lobes separated by narrow postantennal groove; temporal lobes slightly divergent posteriorly; medial, posterior margins of temporal lobes broadly pilose; orbital groove complete; three temporal setae in transverse row near occiput; eye deeply bilobed, strongly constricted at middle (Fig. 210); two pairs of postlabial setae.

Pronotum elongate; length/greatest width 1.61; sides curved; base moderately narrowed, curved; apex strongly narrowed, truncate; median groove dilated, slightly constricted anterior to posterior median pit, closed at base; anterior median pit four times wider than median groove at middle of its length; pit 0.36 of width of pronotum; basal impressions open posteriorly; discal striole nearly straight, reaching middle of pronotum; marginal groove fine, visible in dorsal view; angular seta present; eight or nine marginal setae; two or three basal setae just medial to basal impression; anterior 0.5 of sternopleural groove absent, posterior part represented by three isolated pits (Fig. 211).

Elytra relatively short, broad; striae impressed, punctate; sutural interval depressed below level of others; intercalary stria not abbreviated; intratubercular stria only slightly dilated near apex; preapical tubercle only slightly inflated; apical tubercles more strongly inflated; sutural stria with one seta near apex, one seta in sutural interval posterior, medial to apex of sutural stria; parasutural stria with complete row of eight setae; intercalary stria with complete row of eight setae; intratubercular stria with three or four setae near apex; marginal stria with about 14 setae; apical tubercle with four or five setae; metasternum not sulcate; transverse sulci glabrous, narrowed medially, medial end of each half with small deep pit; sulci of Sternum VI pollinose, widely separated from one another, also from submarginal sulcus; female with slight lateral pit on Sternum IV; male with pair of tubercles posterior to medial ends of transverse sulci on Sterna III, IV, without median sulcus (Fig. 212); male without ventral tooth on anterior femur, without proximal tooth on anterior tibia; middle calcar narrow, prominent, apex obtuse; hind calcar triangular, apex slightly obtuse.

This species is closest to *C. sulcigaster*, but differs in having the median groove of the pronotum closed posteriorly, the posterior part of the sternopleural groove interrupted, and the eye more strongly constricted. The male lacks the median sulcus on abdominal Sterna I-IV which is characteristic of the latter species. We dedicate this species to the collector, Andrew Moldenke, a dedicated coleopterist and our onetime co-worker on Vermont Carabidae.

Clinidium (sensu stricto) sulcigaster Bell 1973

(Figs. 208, 213)

Clinidium (sensu stricto) sulcigaster Bell 1973: 279-282

Type Material.— HOLOTYPE male, labelled: "GUAT. Finca Moca, Santa Barbara, Such., 3000', VI-12-1966, J. M. Campbell" (BSRI, CNC no. 12,700). The locality is in Guatemala, Department of Suchitepéquez, near Lake Atitlán.

Description.— Length 5.5 mm. Stylet elongate, 0.5 of length of antennal Segment XI, compressed, apex slightly oblique; minor setae absent except for Segment XI; basal setae absent; Segments I-IX each with subapical pollinose ring; head longer than broad; median lobe small, shield-shaped; frontal grooves broad, pollinose; temporal, antennal lobes separated by narrow postantennal groove; frontal space narrow; medial margins of temporal lobe parallel; medial margin narrowly pollinose; posterior margin of temporal lobe broadly pilose; orbital groove complete; three temporal setae in orbital groove; eye very small, heavily pigmented, less constricted at middle than in *C. moldenkei*; three pairs of postlabial setae.

Pronotum elongate, length/greatest width 1.68, widest slightly anterior to middle; sides curved anteriorly, oblique, scarcely curved posteriorly; apex narrow, truncate; base moderately narrow, curved; median groove open posteriorly, moderately dilated, about 0.1 of width of pronotum at middle; margins parallel in posterior 0.5 except for slight dilation at posterior median pit, latter equidistant between middle and base of pronotum; anterior to middle, margins divergent to anterior median pit, abruptly narrowed anterior to pit; anterior median pit about 0.33 of width of pronotum; basal impressions narrow, open posteriorly; discal striole nearly straight, reaching nearly to middle of pronotum; marginal groove fine, visible in dorsal view; angular seta absent; three marginal setae present in anterior 0.33 of marginal groove; one basal seta just medial to basal impression; anterior 0.5 of sternopleural groove absent, posterior 0.5 entire.

Elytra relatively short, broad; striae impressed, punctate; sutural interval as convex as Interval II; intercalary stria not abbreviated; intratubercular stria with basal 0.25 effaced; middle portion represented by row of punctures; apical 0.33 impressed; marginal stria entire; preapical tubercle slightly inflated; apical tubercles inflated, contiguous; sutural, parasutural striae without setae; intercalary stria with one seta at base, one in basal 0.5 or absent, and two in apical 0.5; intratubercular stria with two setae near apex; marginal stria with one seta near middle, six setae in apical 0.33; preapical tubercle with two setae; metasternum not sulcate; transverse sulci interrupted medially, each 0.5 pollinose in medial 0.5, glabrous in lateral 0.5; in male, abdomen with median sulcus bounded laterally by paired carinae; sulcus deep, distinct on Sterna II, III, extending anteriorly to include medial part of Sternum I, posteriorly across Sternum IV to end on Sternum V (Fig. 213); male without ventral tooth on anterior femur, without proximal tooth on anterior tibia; middle calcar triangular, dorsal margin angulate, notched; hind calcar narrower, scarcely notched.

Female unknown.

This species differs from *C. moldenkei* in having the intratubercular stria incomplete anteriorly, in having fewer elytral setae and a less constricted, smaller eye. Also, the male has a median sulcus on the anterior 0.5 of the abdomen.

Clinidium (sensu stricto) argus new species
(Fig. 207)

Type Material.— HOLOTYPE male, labelled: "Philippines, Horns of Negros", date and collector not specified (MCZ). The label is similar to that on the holotype of *Omoglymmius (sensu stricto) crassicornis* Bell and Bell. The label on the latter specimen lists the collector as J. W. Chapman. The locality is a mountain on the Island of Negros. This locality is at least questionable.

Description.— Length 6.6 mm. Stylet elongate, 0.4 of length of Segment XI, compressed, apex truncate; minor setae absent except for Segment XI; basal setae absent; Segments I-X each with subapical pollinose ring; head 1.5 longer than broad; median lobe rhomboid; frontal grooves broad, pollinose; antennal lobe small, triangular, separated from temporal lobe by broad, pilose postantennal area; frontal space moderately broad; medial margins of temporal lobes parallel; posterior margin of temporal lobe broadly pilose; orbital groove complete; four or five temporal setae in orbital groove; eye divided into two portions resembling ocelli, anterior eye oval, posterior one smaller, round; two pairs of postlabial setae.

Pronotum elongate; length/greatest width 1.72; widest near middle; sides curved; apex strongly narrowed, truncate; base slightly narrowed, curved; median groove open posteriorly, strongly dilated, 0.16 of width of pronotum at middle; margins parallel, anterior median pit only slightly wider than median groove; basal impression round, closed posteriorly, but connected to lateral margin, median groove by depressed, pollinose areas; discal striole straight, extending to middle of pronotum; marginal groove slightly dilated, visible in dorsal view; angular seta absent; eight to 10 marginal setae; three basal setae medial to basal impression; sternopleural groove nearly complete, interrupted dorsad to coxa.

Elytra relatively long, narrow; sutural, parasutural striae impressed, narrow, conspicuously punctate; intercalary stria wider, deeper than others; intratubercular stria fine, entire; marginal stria entire, strongly dilated posteriorly; preapical tubercle scarcely inflated; apical tubercles strongly inflated, contiguous; sutural stria without setae; parasutural stria with one seta at base, one or two in anterior 0.33; intercalary stria with two setae at base, one laterad to the other, complete row of 10-11; intratubercular stria with four setae in apical 0.33; marginal stria with complete row of about 20 setae; apical tubercle with three setae in conspicuous punctures; metasternum with incomplete median sulcus in anterior 0.5; abdominal sterna with transverse sulci narrowly interrupted in middle; transverse sulci of Sternum VI narrowly separated from submarginal sulcus; Sternum VI with one pair of setae; in male, abdominal Sternum III with median pollinose area, latter continued onto Sternum II; Sternum IV with small median pollinose area; very small, inconspicuous pairs of tubercles posterior to transverse sulci at midline on Sterna III, IV; male without ventral tooth on anterior femur; without proximal tooth on anterior tibia; calcars large, strongly cultrate, curved anteriodorsally, apices recurved.

The divided compound eyes separate this species from all others except the closely related *C. beccarii*, described, possibly erroneously, from New Guinea, and *Rhyzodiastes (Rhyzotetrops) janus* of Fiji. *C. beccarii* has the paramedian grooves much longer, and the calcars are triangular.

Clinidium (sensu stricto) beccarii Grouvelle 1903 NEW COMBINATION
(Fig. 209)

Clinidium beccarii Grouvelle 1903: 140.

Rhyzodiastes beccarii (Grouvelle) Bell and Bell 1978.

Type Material.— HOLOTYPE male, labelled: "Nuovo Guinea: Hatam" (GEN). According to the original description, collected by Beccarii. In 1978 we erroneously assigned this species to *Rhyzodiastes* based on the description. We have not seen this specimen but now have studied detailed sketches of it, kindly supplied by Dr. Poggi.

Description.— Length 8 mm. Head longer than broad; median lobe small, rhomboid; antennal lobe small, separated from temporal lobe by broad postantennal pollinose area; three temporal setae; eye divided into two ocellus-like organs, latter only slightly separated.

Pronotum less elongate than in *C. argus*, length/greatest width about 1.55; median groove broadly dilated, margins parallel; anterior median pit slightly wider than median groove; discal striole much longer than in *C. argus*, reaching almost to anterior median pit.

Male with transverse band of pollinosity connecting transverse sulci in midline on Sternum III; Sternum IV-VI without pollinosity in midline; paired tubercles near middle of Sterna III, IV; calcars triangular, not cultrate.

ADDITIONS, CORRECTIONS TO PARTS I-III, INCLUDING ADDITIONAL SPECIES

Genus *Dhysores* Grouvelle 1903*Dhysores basilewskyi* (Brinck 1965)

Through the courtesy of Dr. Roy Danielsson, we have been able to compare the series of specimens from the former Belgian Congo (42 mi. N. of Kapona) (CAS) with a specimen labelled as a paratype in the collection of the University of Lund. The latter, a male, is labelled: "Tshuapa: Lac Tumba, Mabali, 350 m. (dans humus), N. Leleup 29-IX, 1955". This specimen and locality are not mentioned in the original description, and its status as a paratype is doubtful. Unlike all previous specimens of the genus from the tropical zone in Africa, this one is definitely from a lowland site, and implies that the genus is not limited to montane forests, as we previously thought. It also shows that *D. basilewskyi* has the most extensive range of any member of the genus.

Dhysores biimpressus new species
(Fig. 214)

Type Material.— HOLOTYPE male, labelled: "Usumbara, Neu Bethel, 10.3, 1905, coll. Jul. Moser" (MNHB). PARATYPE one female, same data (MNHB). The locality is in Tanzania, formerly German East Africa. It is a small mountain range, near Lushoto on the Kenyan border.

Description.— Length 6.2-7.2 mm. Anterior tentorial pits large, rounded; prefrontal pits entirely absent; frontal space broader than in other members of genus, nearly as wide as long; frontal grooves scarcely impressed; two pairs of postlabial setae; basal impressions about 0.6 of length of pronotum, anterior part of impression more abruptly narrowed than in *D. quadriimpressus*; hind angles of pronotum denticulate; one marginal seta on pronotum; elytral humeri not especially narrowed, resembling those of *D. basilewskyi* (Brinck) (Bell and Bell, Part II, p. 383); Stria VI represented by row of fine punctures, its anterior fourth effaced; Stria VII impressed except for anterior 0.15, where it is represented by row of punctures; elytral setae unusually long.

In our key to species of *Dhysores* (Part II, p. 382), this species will trace to Couplet 2, where it will not fit either alternative, since the anterior tentorial pits are large and round, while the prefrontal pits are entirely absent. The absence of the prefrontal pits and the broader frontal space separate it from the sympatric *D. quadriimpressus* (Grouvelle). The most similar species is probably *D. thoreyi* (Grouvelle), of South Africa, but in the latter species the anterior tentorial pits are small and oblique, while the prefrontal pits are at least suggested, and the humeri are markedly narrowed.

Dhysores quadriimpressus (Grouvelle)

We have seen 14 additional specimens of this species (all in MNHB), eight from Neu Bethel, the type locality for *D. biimpressus*, and six from Ost Usumbara, coll. Methner. Dr. Basilewsky has informed us that we confused the type locality, Usumbara, with Usumbura (now Bujumbura) in Burundi. It is actually in northeast Tanzania and is the same as that of *D. biimpressus*. We are grateful to Dr. Basilewsky for clearing up the confusion.

Genus *Kupea* Bell and Bell 1982

This name was substituted for *Kupea* Bell and Bell 1978, which is preoccupied by *Kupea* Philpott 1930.

Kupeus arcuatus (Chevrolat 1873a) NEW COMBINATION

R. M. Emberson (personal communication) has pointed out that two of the localities listed by us, Reefton and Springs Junction, are on the South Island of New Zealand. However he has indicated that the Springs Junction label is an invalid one. If the Reefton record (BMNH) is correct then this would be the only record of a rhyssodine from the South Island.

GENUS *KAVEINGA* BELL AND BELL 1978*Kaveinga (sensu stricto) occipitalis* (Grouvelle 1903)

Rhyssodes occipitalis Grouvelle 1903: 105-106.

Type Material.— LECTOTYPE male (here designated), labelled: "NUOVA GUINEA, Fly River, L. M. D'Albertis 1876-1877" (GEN). PARALECTOTYPES two males, two females, same label as lectotype (GEN); one female, same label as lectotype (MNHN). We erroneously listed the latter specimen as a holotype (Part II:406).

The hind calcar of the male of *K. occipitalis* is very small and acute, similar to that of *K. strigiceps* Bell and Bell.

Kaveinga (sensu stricto) poggii new species

(Fig. 215)

Type Material.— HOLOTYPE male, labelled: "Is. Goodenough:Gennaio 1890, L. Loria" (GEN). This island is one of the D'Entrecasteaux Group, north of the eastern tip of New Guinea.

Description.— Length 4.8 mm. Antennal Segment I pollinose dorsally; Segments II-V each with narrow pollinose band; basal setae sparse on Segment VII, more numerous on VIII-X.

Head as long as wide, clypeus broadly separated from median lobe by band of pollinosity; parafrontal boss small, nearly circular, separated from antennal rim and from median lobe by broad bands of pollinosity, and bordered posteriorly by pollinose band; sides of median lobe broadly emarginate; orbital groove short, narrowed posteriorly, ending opposite middle of eye; temporal lobe slightly wider than long; anteriomedial margins oblique, converging posteriorly; medial angle obtuse, narrowly overlapped by median lobe; temporal setae one or two (right anterior one absent from holotype); anterior seta in orbital groove; posterior one in round pollinose fovea in temporal lobe; postorbit entirely pollinose; temporal lobe with distinct overhang in lateral view; suborbital tubercle and gular ridge absent.

Pronotum relatively short, broad, length/greatest width is 1.15; widest anterior to middle; sides strongly curved and convergent between widest point and apex; sides oblique, slightly convergent from widest point to hind angles, margin not sinuate anterior to hind angle; latter obtuse; shallow emargination present between hind angle and base; basal knob small, depressed, pollinose; paramedian grooves deep, pollinose, width at middle nearly equal to that of outer carina; anterior end of inner carina pollinose, so that glabrous area appears abbreviated anteriorly; posterior tip of inner carina acutely pointed; marginal grooves broad; marginal seta absent; angular seta present; prosternum with shallow transverse groove between precoxal carinae; latter not quite reaching anterior margin of pronotum.

Elytra moderately broad, slightly flattened; humeral tubercles not exerted; striae deep, pollinose; intervals convex, subcarinate; stria punctures coarse, each puncture about 0.5 as wide as interval; Stria II with one basal seta, three setae in apical fourth; Stria IV with six setae; apical stria without setae; several setae near apex of Stria VII; abdominal Sterna III-V each with coarsely punctate, pollinose transverse sulcus, latter not interrupted at midline; femora with pollinose bands; serrulation of middle tibia well developed; hind calcar of male slender, but its extreme tip narrowly truncate; female unknown.

This species is named for Dr. Roberto Poggi of the Museo Civico di Storia Naturale "G. Doria" of Genoa, in gratitude for the help he has given us during this study.

In our Key to *Kaveinga s. str.*, this species will trace close to *K. abbreviata*. Therefore, the key should be modified to read as follows:

- | | | | |
|-----|-----|--|------------------------------|
| 3 | (2) | Pronotum relatively short, broad; length/greatest width 1.15 or less | 3.1 |
| 3' | | Pronotum elongate, length/greatest width 1.2-1.3 | 4 |
| 3.1 | (3) | Parafrontal boss small, round, separated from antennal rim and from median lobe by broad pollinose bands; inner carina of pronotum acutely pointed posteriorly | <i>K. poggii</i> new species |

- 3.1' Parafrontal boss large, triangular, separated from antennal rim and from median lobe by linear pollinose bands; inner carina of pronotum obtusely pointed posteriorly *K. abbreviata* (Lea)

K. poggii clearly belongs to Group I, the species with deep, pollinose striae and subcarinate intervals. The short pronotum makes it most similar to *K. abbreviata*, but it differs from the latter in having the middle tibia strongly serrulate, the inner pronotal carina acutely pointed posteriorly, and the parafrontal boss small and round.

The remaining members of the Group have the pronotum more elongate. *K. fibulata* differs in having the hind angles of the pronotum rounded, while the four species of the *K. pignoris* complex lack the parafrontal boss. *K. poggii* appears to be intermediate between *K. abbreviata* and the remaining members of Group I, and makes it appear more likely that the group is monophyletic.

GENUS *GROUVELLINA* BELL AND BELL 1978

Grouvellina hexadon new species (Figs. 216, 220)

Type Material.— HOLOTYPE male, labelled: "COMORES, Mayotte Mamouzou, 13-8-69, s/ecorces, a la lumiere, Y. Gomy" (GVA)

Description.— Length 4.8 mm. Antennal Segment XI slightly longer than wide; apical stylet short, acute; tufts of minor setae on Segments V-X; antennal Segment I extensively pollinose in dorsal aspect; Segments II-X with two transverse pollinose bands, basal band interrupted in Segments VIII-X; head as wide as long, frontal, postantennal grooves deep, relatively narrow; median lobe rather narrow, broadly rounded posteriorly; parafrontal bosses narrow, rather long, temporal lobe as wide as long, sinuate anterior to medial angles, latter narrowly separated, obtusely pointed; two temporal setae; four labral setae; orbital groove complete, broadly pilose; two pairs of postlabial setae; mentum pollinose; postmentum contrastingly glabrous.

Pronotum moderately long, length/greatest width 1.35; lateral margins nearly parallel; base and apex slightly narrowed; outer carina not bent outwards at base; three or four marginal setae; prosternum without precoxal carinae except for trace just anterior to coxa.

Elytral striae deep, very coarsely punctate; intervals broader than striae, not carinate; base of Interval II elevated, forming small tooth (as in *G. edentata*); humerus prominent, quadrangular, with conspicuous patch of golden pilosity; Stria I with two setae near apex; Stria II with eight setae; Stria IV with six setae; Stria VII with about nine setae in its apical 0.2; metasternum entirely coarsely punctate without lateral pollinosity.

Male with ventral tooth on all femora; male with very minute prominent tooth on anterior tibia (Fig. 220); male with hind calcar truncate at tip.

This species is smaller than any other member of the genus. In our key (Part II: 411-413), it traces to couplet 6. The presence of a ventral tooth on all femora and the small size will differentiate it from both species at this couplet. The absence of a precoxal carina is an additional difference from *G. tubericeps*. It otherwise is almost a miniature of the latter species, to which it appears to be related.

This species is not *Rhysodes planifrons* Fairmaire 1893, the only Rhysodine previously described from the Comoro Islands. We have not been able to locate the type for the latter species, which we suspect of being a *Grouvellina*, but the original description indicates that the parafrontal bosses are united to the median lobe, and the length is given as 8mm.

GENUS *YAMATOSA* BELL AND BELL 1981

A misprint is present in the description of the genus (Part II:424). Setae are present in apex of Striae IV and VII or else are limited to apex of Stria VII.

A specimen labelled "Java, J. D. Pasteur 268-94", (MNHN) is labelled as a type of "Rhysodes v. longior". (now *Yamatosa longior*). It is not conspecific with the remaining types, but is *Omoglymmius* (*Hemiglymmius*) *rimatus* Bell and Bell (Part III, p.139).

The discovery of two additional species makes it necessary for us to revise our summary of the phylogeny of this genus, and to alter the key to species. *Y. kryzhanovskyi* is perhaps the most isolated species in the genus. It differs from all other species in having the prothoracic pleuron and the disc of the metasternum coarsely punctate. The absence of the "beard" on the labium links it to the "western" line, while the presence of the antennal stylet is a common character with the "eastern" line. *Y. kabakovi*, on the other hand, clearly belongs to the "eastern" line, and is closest to *Y. niponensis*.

KEY TO SPECIES

- 1 Prothoracic pleuron impunctate; punctures of metasternum limited to margin 2
- 1' Prothoracic pleuron densely punctate; metasternum with numerous punctures on disc, in addition to row along each lateral margin
..... *Yamatosa kryzhanovskyi* new species
- 2 (1) Segment XI with distinct apical stylet; both eye and marginal groove of pronotum fully developed 3
- 2' Segment XI of antenna obtuse, without apical stylet; either eye reduced or else marginal groove of pronotum reduced 7
- 3 (2) Prosternum with distinct precoxal carina; discal striole ended at or posterior to middle of pronotum 4
- 3' Prosternum without precoxal carinae; discal striole ended at, or anterior to apical third of pronotum 5
- 4 (3) Precoxal carina extended more than 0.75 of distance from coxa to anterior margin of pronotum; discal striole 0.5 of pronotal length
..... *Yamatosa longior* (Grouvelle) (Part II, p. 425)
- 4' Precoxal carina extended about 0.33 of distance from coxa to anterior margin of pronotum; discal striole 0.33 of pronotal length
..... *Yamatosa peninsularis* (Arrow) (Part II, p. 427)
- 5 (3') Frontal and antennal grooves narrow, equal in width to posterior part of clypeal grooves; posterior margins of frontal, antennal grooves sharply defined; discal striole ended at or slightly anterior to middle of pronotum 6
- 5' Frontal and antennal grooves dilated, much wider than posterior part of clypeal grooves; posterior margins of frontal and antennal grooves not sharply defined; discal striole extended nearly to anterior margin of pronotum *Yamatosa arrowi* (Grouvelle) (Part II, p. 428)
- 6 (5) Punctures of elytral striae I-V rounded, hind calcar of male triangular, pointed *Yamatosa niponensis* (Lewis) (Part II, p. 427)
- 6' Punctures of elytral striae I-V elongate; hind calcar of male obtuse, with dorsal "shoulder" *Yamatosa kabakovi* new species
- 7 (2') Marginal groove of pronotum absent except in basal fourth of pronotum; eyes large, much deeper than long
..... *Yamatosa reitteri* (Bell) (Part II, p. 429)

- 7' Marginal groove of pronotum nearly complete, ended short distance from anterior margin of pronotum; eyes more or less reduced 8
- 8 (7') Head evenly rounded posteriorly, widest point just posterior to eye; eye only moderately reduced, deeper than long, with about 100 ommatidia *Yamatosa draco* (Bell) (Part II, p. 429)
- 8' Head broadened posteriorly, widest point far posterior to eye; eye markedly reduced, longer than deep, with about 50 ommatidia *Yamatosa boysi* (Arrow) (Part II, p. 430)

Yamatosa kryzhanovskyi new species
(Figs. 217, 222)

Type Material.— HOLOTYPE male, labelled: "Vietnam, mts. NE Thai, Nguen, 12-1-1964, Kabakov" (LEN). PARATYPE one female, same data as holotype (LEN).

Description.— Length 5.9-6.3 mm. Antennal Segment XI with slender, acuminate stylet; head cordate; anterior tentorial pits rather small, punctiform; frontal grooves narrow, well defined; median lobe short, its tip rather broadly truncate; eye large, deeper than long; mentum with a few punctures near middle, not "bearded" in either sex; one pair of postlabial setae present.

Pronotum moderately elongate, length/greatest width 1.39; base only slightly narrowed; apex markedly narrowed, discal striae long, extending about 0.67 length of pronotum; marginal groove complete; propleura sparsely, coarsely, shallowly punctate (Fig. 222); prosternum with transverse band of punctures anterior to coxae; precoxal carinae absent.

Elytra relatively broad for genus, slightly flattened; striae punctures relatively coarse, close together, separated by less than diameter of one of them; elytral intervals convex; Striae I-VI scarcely abbreviated at base; basal portions of V, VI punctate but not impressed; Stria VII effaced in basal third, middle third represented by punctures but not impressed; apical third impressed, punctate; setae absent from Stria IV; metasternum with punctures on disc as well as margins; female with small, shallow lateral pit on Sternum IV.

Anterior femur with ventral tooth in both sexes; anterior tibia of male with medial groove, latter bounded both anteriorly and posteriorly near base by pair of flanges; spurs of middle, hind tibiae nearly equal; hind calcar small, obtuse, its tip just above level of spurs.

This species is unique within the genus in having the prothoracic pleura and the disc of the metasternum punctate. It differs in addition from the sympatric *Y. kabakovi* in having the elytral striae with coarse, crowded punctures, elytral Striae I-VI not abbreviated at base, the mentum without a beard, the tip of the median lobe broadly truncate, and the pronotum broader and less sharply narrowed to apex.

It is a pleasure to name this species for Dr. O. Kryzhanovsky, whose courtesies made it possible for us to study specimens in the Leningrad collection.

Yamatosa kabakovi new species
(Figs. 218, 223)

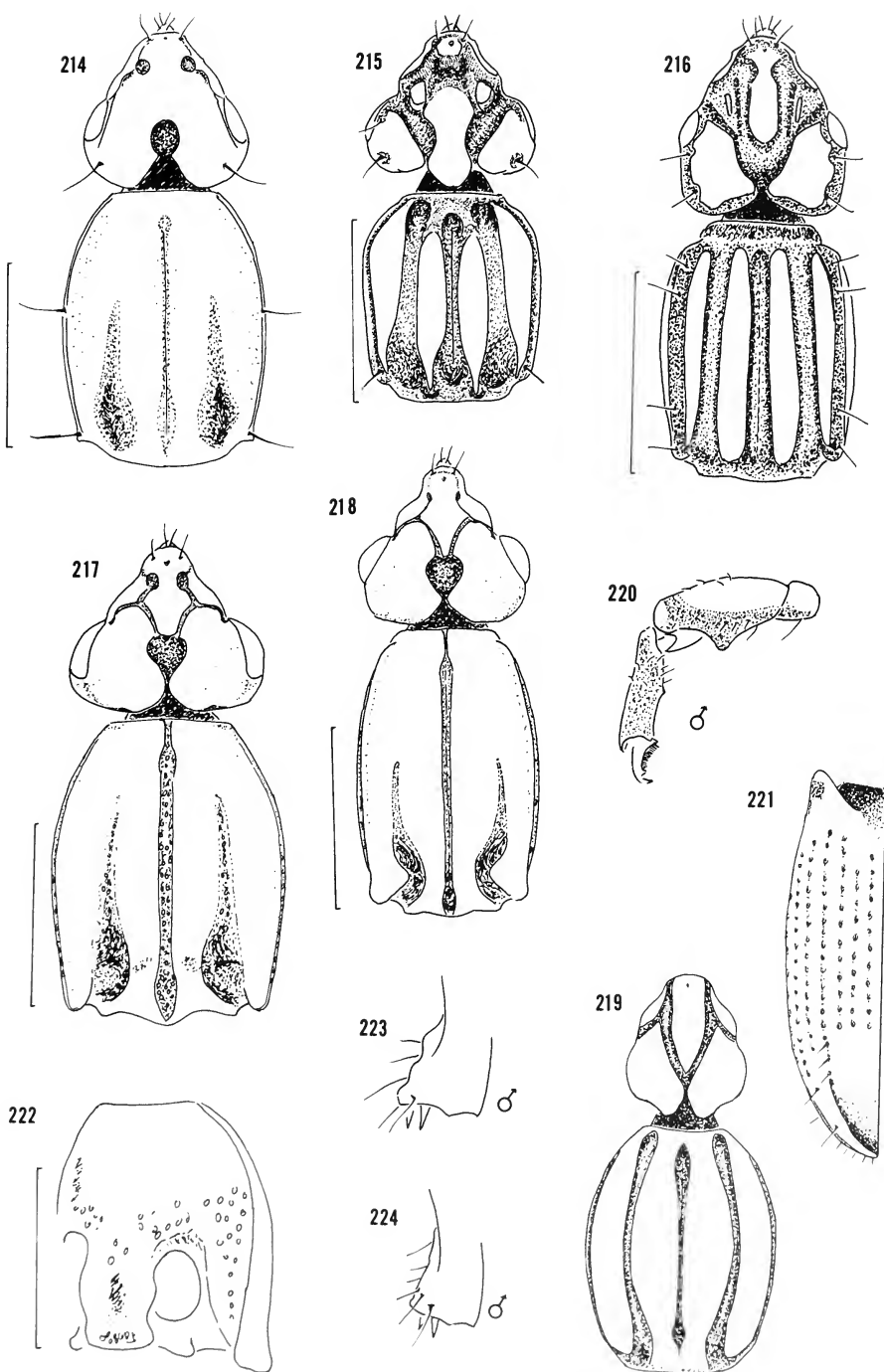
Type Material.— HOLOTYPE male, labelled: "Vietnam, mountains of Sha-Pa Province, 1600-2000 mm., 5.8, 1962, coll. O. N. Kabakov" (LEN).

Description.— Length 6.0 mm. Antennal Segment XI with apical stylet distinct, though small; head cordate; anterior tentorial pits small, punctiform; frontal grooves narrow, well defined, median lobe short, its tip narrowly pointed; eye large, deeper than long; mentum conspicuously punctate and "bearded" in male (female unknown); one pair of postlabial setae present.

Pronotum elongate, narrow, length/greatest width 1.59; sides nearly parallel except anteriorly; apex distinctly narrowed; base scarcely narrowed; discal striae ends slightly anterior to middle of pronotum; marginal groove of pronotum complete; precoxal carina absent; prothoracic pleuron impunctate; prosternum impunctate, including precoxal area.

Elytra very narrow, cylindrical; Striae I-IV impressed, punctate, punctures longer than wide; Striae V-VII not impressed, represented by fine, widely spaced, round punctures; Stria I with base entire; Striae II, III with base slightly abbreviated; Striae IV, V effaced in basal 0.20; Stria VI effaced in basal 0.25 and also near apex; Stria VII effaced in basal 0.33, its extreme apex impressed; setae confined to apex of Stria VII.

Plate 18. Figs. 214–219. Head and pronotum, dorsal aspect. Fig. 214, *Dhysores biimpressus* new species; Fig. 215, *Kaveinga* (*s. str.*) *poggii* new species; Fig. 216, *Grouvellina hexadon* new species; Fig. 217, *Yamatosa kryzhanovskyi* new species; Fig. 218, *Yamatosa kabakovi* new species; Fig. 219, *Arrowina punctatolineata* (Grouvelle) (redrawn from sketch by R. Poggi); Fig. 220, Anterior leg (excluding tarsus), male, *Grouvellina hexadon* new species; Fig. 221, Left elytron, dorsal aspect, *Arrowina punctatolineata* (Grouvelle); Fig. 222, Prothorax, left ventrolateral aspect, *Yamatosa kryzhanovskyi* new species; Figs. 223–224, Hind tibia, apex, male; Fig. 223, *Yamatosa kabakovi* new species; Fig. 224, *Y. niponensis* (Lewis).



Metasternum with row of punctures along lateral margin but without punctures on disc; metasternum of male shallowly impressed; abdominal Sternum IV of male with shallow lateral pit (female unknown).

Anterior femur of male with ventral tooth (female unknown); anterior tibia of male with medial groove bordered by small but distinct flanges near base; spurs of middle and hind tibiae nearly equal; hind calcar of male forming acute angle above spurs, its proximal margin with distinct "shoulder".

This slender, nearly cylindrical species has the elytral striation more reduced than in any other member of the genus. It is closely related to *Y. niponensis* Lewis (Fig. 224) but differs from the latter species in being narrower and more cylindrical with the pronotum more elongate, and with the elytral striae more reduced. In the male, the form of the hind calcar will separate the two species (Fig. 223).

This species is named for the collector, O. N. Kabakov.

Yamatosa longior (Grouvelle 1903)

In MNHN, there is an additional locality record, a specimen from Mt. Ardjoena, Java, Coll. Mme. E. Walsh.

GENUS *ARROWINA* BELL AND BELL 1978

In Parts I and II, we did not include *Rhysodes punctatolineatus* Grouvelle, as we did not know the location of the type, and were not able to learn the correct generic placement from the original description. We have since discovered that it is in the Museo Civico di Storia Naturale in Genoa. The curator, Dr. Roberto Poggi, has very kindly furnished us with detailed drawings and notes which make it clear, as he indicated, that it belongs in *Arrowina*. The range of the genus, as stated in Part I, p. 71, must be amended to read "Ceylon, southern India, Sumatra and Japan". Phylogenetically, *A. punctatolineata* is most closely related to *A. taprobanae* and *A. pygmaea*. The latter two species are closer together than either is to *A. punctatolineata*, however.

REVISED KEY TO SPECIES (Supersedes that of Part II, pp. 438-439)

- 1 Head almost twice as long as wide; anterior femur of male with ventral tooth (female unknown) *Arrowina rostrata* (Lewis) (Part II, p. 439)
- 1' Head only slightly longer than wide; anterior femur of male without ventral tooth (male unknown in *A. punctatolineata*) 2
- 2 (1) Orbital groove absent; lateral margin of inner pronotal carina sloped gradually into paramedian groove 3
- 2' Orbital groove complete, somewhat dilated; lateral margin of inner carina vertical, sharply defined 5
- 3 (2) Metasternum with a few punctures on anterior margin, otherwise impunctate; eye reduced; elytral striae not impressed, represented only by rows of punctures which become obsolete both near base and near apex *Arrowina punctatolineata* (Grouvelle)
- 3' Metasternum with row of coarse punctures along each lateral margin; eye not reduced; elytral striae distinctly impressed, punctate from base to apex 4
- 4 (3') Metasternum with punctures confined to lateral margins; length 5.0 mm or more *Arrowina taprobanae* (Fairmaire) (Part II, p. 439)
- 4' Metasternum with punctures in middle as well as along lateral margins;

- length 4.3 mm or less *Arrowina pygmaea* Bell and Bell (Part II, p. 441)
- 5 (2') Eyes large, deeper than long; posteriomedial margin of temporal lobe sinuate posterior to medial angles *Arrowina nilgiriensis* (Arrow) (Part II, p. 441)
- 5' Eyes reduced, longer than deep; posteriomedial margin of temporal lobe not emarginate *Arrowina anguliceps* (Arrow) (Part II, p. 442)

Arrowina punctatolineata (Grouvelle 1903) NEW COMBINATION
(Figs. 219, 221)

Rhysodes punctatolineatus Grouvelle 1903: 116.

Rhysodes punctatostriatus Grouvelle 1903: 97, 143 (error).

Rhysodes punctolineatus Hincks 1950: 11 (error).

Type Material.— HOLOTYPE female, labelled: "SUMATRA: Mte. Singalang" (GEN). (Specimen deformed on right anterolateral margin of pronotum)

Description.— Length 6.8 mm. Antennal Segment XI slightly longer than wide; stylet minute, scarcely evident; head slightly longer than wide; rostrum not elongate; median lobe elongate, pointed posteriorly; frontal space scarcely evident; medial angles obtusely rounded, nearly contiguous; posteriomedial margin of temporal lobe rounded; posteriolateral margin distinctly emarginate; orbital groove absent; eye reduced, longer than deep, strongly pigmented and difficult to see; postorbital tubercle present, though very obtuse.

Pronotum elongate, length/greatest width about 1.3; widest at middle, sides evenly curved, apex and base both markedly narrowed; inner carina slightly wider than outer one; inner carina with lateral margin ill-defined, sloped gradually into paramedian groove.

Elytra with sides parallel in middle third; humeral region more narrowed than in *A. taprobanae*; elytral striae not impressed, represented only by rows of very fine punctures; striae punctures obsolete in basal 0.15 and apical 0.33; base of elytron obliquely depressed, forming triangular depression in region of scutellum; elytron with three setae in posterior part of Stria IV and several setae on lateral face of apical tubercle, and several setae in apex of Stria VII; metasternum with row of punctures along anterior margin, otherwise impunctate (Fig. 221); middle and hind tibiae with spurs nearly equal.

This distinctive species differs from other known members of the genus in the reduction of the elytral striation and in the triangular depression at the bases of the elytra. The reduction of the eye is a feature in common with *A. anguliceps*, but it differs from the latter species in the absence of the orbital grooves, as well as in the shape of the temporal lobes, and in the virtual absence of the frontal space.

SUBGENUS *PYXIGLYMMIUS* BELL AND BELL 1978

We have found an additional species from Sumatra. In the key it would trace to *O. hesperus*. The key can be modified as follows:

- 7 (6') Postorbital tubercles large, prominent; paramedian grooves relatively shallow 7.1
- 7' Postorbital tubercles relatively small, not prominent in dorsal view; paramedian grooves deep, more sharply defined *O. strabus* (Newman)
- 7.1 (7) Elytral intervals flat; intervals, pronotal carinae, temporal lobes strongly microsculptured in female, lateral pit of Sternum IV longitudinally striate, brace weakly developed *O. opacus* new species
- 7.1' Elytral intervals convex; intervals, pronotal carinae, temporal lobes shining, without microsculpture; in female, lateral pit of Sternum IV not striate,

brace strongly developed *O. hesperus* Bell and Bell

Omoglymmius (Pyxiglymmius) opacus new species
(Figs. 225, 234)

Type Material.— HOLOTYPE female, labelled: "Sumatra, Padang, 1890, Modigliani" (GEN).

Description.— Length 9.0 mm. Antennal Segment XI slightly wider than long, tip obtuse; basal setae apparently absent (though possibly lost from holotype); head slightly longer than wide, large relative to pronotum, as in *O. strabus*; clypeus punctate, pollinose, continuous with median lobe; latter rhomboid, wider than long; posterior angle obtuse, anteriomedial margin of temporal lobe oblique; first medial angles distinctly, though narrowly separated; second medial angles contiguous; occipital angles very obtuse though distinct; posteriolateral margin of temporal lobe slightly oblique; each temporal lobe with two coarse punctures; temporal lobes coarsely microsculptured, opaque; postorbit concave dorsad to postorbital tubercle, postorbital tubercle large, 0.7 as long, 0.6 as deep as eye; tubercles less divergent than in *O. hesperus*, width across tubercles slightly greater than width across eyes.

Pronotum short; length/greatest width 1.26; widest point near middle, apex less strongly narrowed than in *O. hesperus*; base moderately narrowed; lateral margin scarcely sinuate anterior to hind angles; paramedian grooves broad, shallow, punctate; paramedian groove equal in width to inner carina at middle, narrower than outer one at middle; both carinae strongly microsculptured, coarsely, densely punctate; marginal groove fine, about 0.20 as wide as outer carina at middle.

Elytra longer, narrower than *O. hesperus*, but shorter than in *O. strabus*; stria punctures relatively coarse; one seta in apical 0.33 of Stria IV; subapical striole with seta; about four in apical 0.5 of Stria VII; elytral intervals strikingly flat, densely microsculptured; female with deep lateral impression in posterior 0.67 of metasternum; female with margin of elytron angulate opposite hind coxa; female with indistinct lateral pits on Sternum I, large lateral pits on Sternum IV, latter separated medially by about twice width of one of them; lateral pit with slight trace of anteriolateral brace, with elongate punctures suggesting longitudinal striation.

Male unknown.

The heavy microsculpture separates this species from *O. strabus* and *O. hesperus*. The very flat elytral intervals are also distinctive. In the proportions of the body and size of postorbital tubercles, it is intermediate between *O. strabus* and *O. hesperus*. The lateral pits of Sternum IV differ from either. *O. hesperus* has a very strong brace but no trace of longitudinal striation, while *O. strabus* has a prominent brace and strong longitudinal striation.

SUBGENUS *ORTHOGLYMMIUS* BELL AND BELL 1978

Omoglymmius (Orthoglymmius) feae (Grouvelle 1895b)

Dr. Poggi has kindly allowed us to study an additional specimen from the Genoa Museum also labelled as a type. We hereby designate the specimen cited as holotype in Part III (female, labelled: "Burma. Charin Cheba. 900-1100 m., X-88, coll. L. Fea" (MNHN)) as LECTOTYPE. The PARALECTOTYPE is a male with same data as lectotype (GEN). It has a pollinose postorbital tubercle, and is possibly not conspecific with the lectotype. Additional material is needed in this difficult subgenus.

SUBGENUS *OMOGLYMMIUS SENSU STRICTO* GANGLBAUER 1892

Three new species *O. gressitti*, *O. craticulus* and *O. largus* are described below.

Omoglymmius (sensu stricto) gressitti new species

(Fig. 229)

Type Material.— HOLOTYPE male, labelled: "PAPUA NEW GUINEA, Wau, Mt. Missim 1500 m. Feb. 25, 1982, R. T. Bell" (BPBM).

Description.— Length 7.9 mm. Antennal segments I-IV coarsely punctate; outer segments with punctures very fine; Segment XI impunctate; head slightly longer than wide; median lobe broad, apex broadly rounded; frontal space broad, U-shaped, its lateral margins strongly curved; medial angles rounded, well separated; posteriomedial margin oblique, slightly concave; posteriolateral margin nearly evenly curved; occipital angle obtuse; antennal lobes glabrous; posteriomedial margin, occipital angle pollinose; orbital groove narrow, very short, ended anterior to middle of eye; temporal lobe with about 25 rather coarse punctures; one temporal seta; small postorbital tubercle present; eye large, round.

Pronotum short, length/greatest width 1.07; widest near middle; base slightly narrowed; apex strongly narrowed; lateral margins strongly curved; margin slightly sinuate anterior to hind angle; inner carina almost twice as broad as outer carina at middle; outer carina widest at middle, narrowed to apex; narrowed nearly to base, but broadened at extreme base; outer carina relatively narrow, lateral and medial margins nearly parallel, so carina of nearly even width, strongly curved; inner carina impunctate; outer carina with about 40 moderately fine punctures; pronotum without setae; prosternum without precoxal carinae.

Elytron moderately long, narrow; striae not impressed; stria punctures coarse; base of Stria IV with longitudinal scarp; transverse basal scarp shining, not pollinose; subapical stria with one seta; Stria VII with one or two setae near apex; metasternum bluish, opalescent, punctate in midline, along margins, part of disc impunctate; abdominal Sterna III-V with punctures, fine, nearly in single line near midline, scattered, coarse near lateral margins; male with rather deep, semicircular lateral pits on Sternum IV; male with small ventral tooth on anterior femur; middle calcar minute; hind calcar larger, obtuse.

This is a large species with a minute postorbital tubercle. It is similar to *O. follis*, also found near Wau, but differs in having a very narrow, heavily punctate outer carina. This species is dedicated to the memory of J. L. Gressitt and his wife, Margaret, for their kind hospitality and assistance on our field trip to the Wau Ecological Institute, Papua New Guinea.

In our world key, this species would trace to couplet 69. The key should be changed as follows:

- | | | |
|--|----------------------------------|------|
| 69 (68) (unchanged) | <i>O. quadraticollis</i> (Arrow) | |
| 69' (unchanged) | | 69.1 |
| 69.1(69') Outer carina narrow, curved, densely punctate .. | <i>O. gressitti</i> new species | |
| 69.1' Outer carina not conspicuously narrower than inner carina, sparsely punctate or impunctate | | 70 |

In our key to species from New Guinea, this species would trace to couplet 18 and should be changed as follows:

- | | | |
|--|---------------------------------|------|
| 18 (17) Outer carina relatively narrow, curved | <i>O. gressitti</i> new species | |
| 18' Outer carina relatively broad, less curved | | 18.1 |
- (Couplet 18 of the original key is to be renumbered as 18.1)

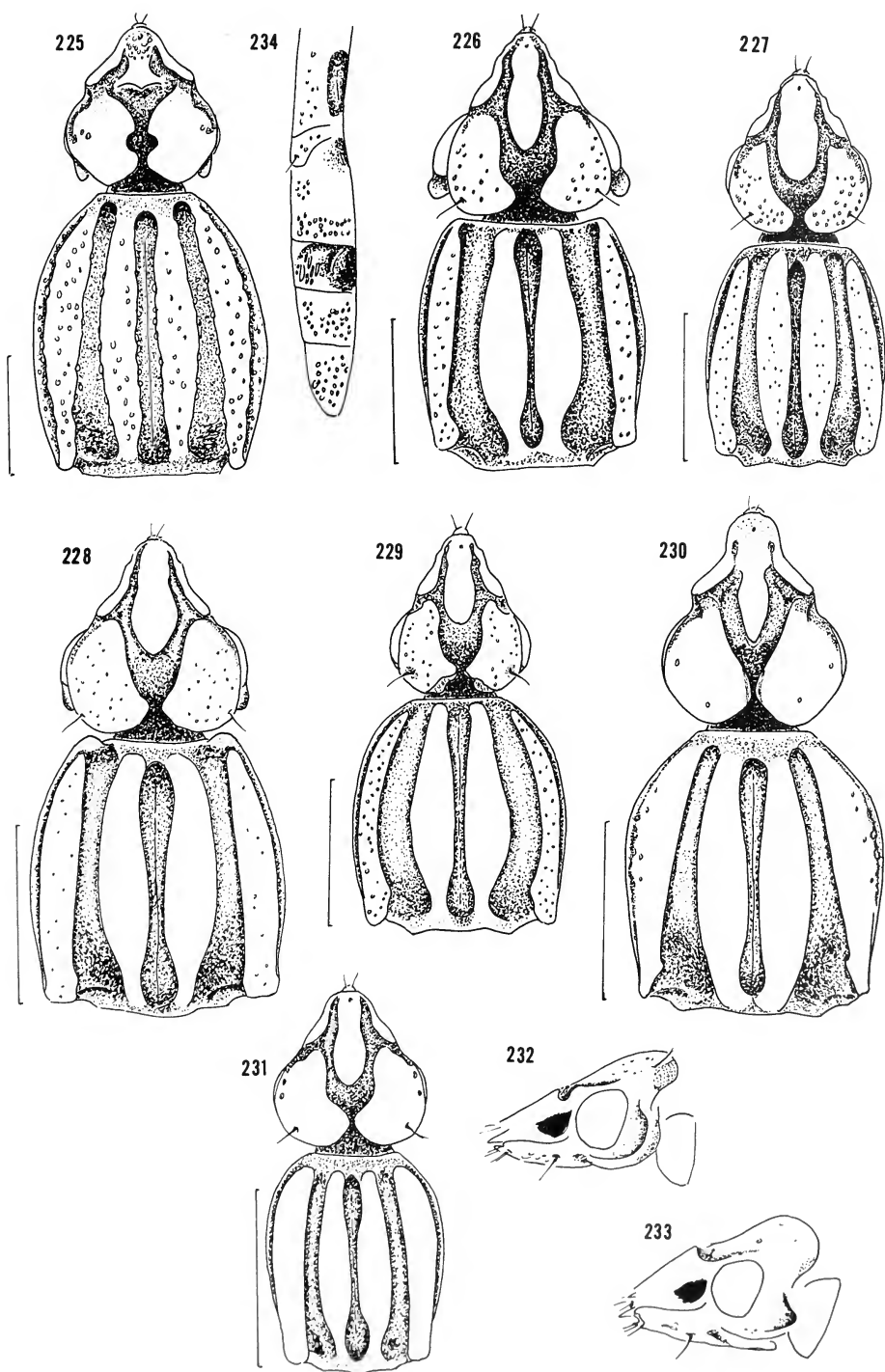
Omoglymmius (sensu stricto) craticulus new species

(Figs. 227, 232)

Type Material.— HOLOTYPE female, labelled: "N. Guinea, S. E., Moroka 1300 m., Loria, VII-XI, 93" (GEN). It had been labelled as *R. capito* Grouvelle.

Description.— Length 7.0 mm. Antennal Segments I-X punctate, outer segments finely so; Segment XI with a few punctures; head slightly longer than wide; median lobe short, broad, tip rounded; frontal space slightly wider than long, its margins curved; medial angles rectangular; posteriomedial margin emarginate; occipital angle very obtuse; posteriolateral margin more strongly, evenly curved, than in *O. planiceps*; orbital groove fine, extending nearly to posterior

Plate 19. Figs. 225–234. Genus *Omoglymmius*. Figs. 225–231, Head and pronotum, dorsal aspect; Fig. 225, *O. (Pyxiglymmius) opacus* new species; Fig. 226, *O. (s. str.) largus* new species; Fig. 227, *O. (s. str.) tolai* new species; Fig. 228, *O. (s. str.) craticulus* new species; Fig. 229, *O. (s. str.) gressitti* new species; Fig. 230, *O. (Laminoglymmius) perplexus* new species; Fig. 231, *O. (Navitia) peckorum* new species; Figs. 232–233, Head, left lateral aspect; Fig. 232, *O. (s. str.) craticulus* new species; Fig. 233, *O. (Laminoglymmius) perplexus* new species; Fig. 234, Metasternum, abdomen left lateral aspect, *O. (Pyxiglymmius) opacus* new species.



margin of eye; temporal lobe with about 20 very fine punctures; one temporal seta, arising from puncture at margin of temporal lobe posterior to eye; posterior face of temporal lobe without pollinosity, but with area of strong microsculpture resembling grid; temporal lobe relatively convex in lateral view; postorbital tubercle short but very deep; eye large, round.

Pronotum very short, length/greatest width 1.05; widest near middle; base slightly narrowed; apex strongly narrowed; lateral margins slightly curved posteriorly; strongly curved, narrowed anteriorly; margin scarcely sinuate anterior to hind angle; marginal groove not dilated; in dorsal view, outer carina appears about 0.6 as wide as inner carina at middle; outer carina convex, directed dorsolaterad so it appears narrower in dorsal than in dorsolateral view; medial margin of outer carina shallowly sinuate just anterior to base; outer carina widest at base; inner carina strongly narrowed at base; inner carina impunctate; outer carina with many exceedingly fine punctures, not evident except under high magnification; pronotum without setae; prosternum without precoxal carinae.

Elytra moderately long; striae not impressed, represented by rows of round, relatively coarse punctures; base of Stria IV with longitudinal pollinose scarp; Stria IV with one seta near apex; subapical stria with one seta; marginal stria with apex impressed, with three or four setae; metasternum with broad medial, lateral bands of punctures, surrounding elongate impunctate space on either side of disc; abdominal Sterna III-VI with many scattered punctures; female with moderately deep, round lateral pit on Sternum IV; female without ventral tooth on anterior femur; male unknown.

The grid of microsculpture on the posterior face of the temporal lobe separates this species from all except *O. planiceps* Bell and Bell. The latter species has much finer, sparser striae punctures which are elliptical, rather than round. In addition, the temporal lobes are much more strongly flattened than in *O. craticulus* and the pronotum is shaped differently.

This species would trace to Couplet 19 in our key to *Omoglymmius sensu stricto* of New Guinea. The punctuation of the metasternum is equivocal, so the key should be altered as follows:

- | | | |
|-----------|---|-----------------------------------|
| 19 (17') | Posterior face of temporal lobe pilose or scaly; temporal seta not marginal . . . | 19.2 |
| 19' | Posterior face of temporal lobe with microsculpture in grid pattern;
temporal seta marginal | 19.1 |
| 19.1(19') | Strial punctures relatively large, round, separated from neighboring
punctures by about 0.5 of length of one of them; temporal lobe relatively
convex | <i>O. craticulus</i> new species |
| 19.1' | Strial punctures small, elliptical, separated by more than length of one of
them; temporal lobe strongly flattened | <i>O. planiceps</i> Bell and Bell |
| 19.2(19) | Metasternum with punctures limited to midline, margins | 20 |
| 19.2' | Metasternum with punctures scattered over entire disc | 23 |

Omoglymmius (sensu stricto) largus new species

(Fig. 226)

Type Material.— HOLOTYPE female, labelled: "NOUVA GUINEA, Fly River, L. M. D'Albertis, 1876-77" (GEN). The specimen also bears a pink label "6880".

Description.— Length 7.2 mm. Antennal Segments V-X coarsely punctate; Segment XI missing in holotype; head slightly broader than long; median lobe lance-shaped, broader anteriorly than in *O. capito*, tip obtuse; frontal space broader than long, lateral margin shallowly sinuate; medial angles rounded, more widely separated than in *O. capito*; posteriomedial margin curved into posteriolateral margin; occipital angle absent; antennal groove rather narrow, not expanded laterally; orbital groove shallow, ill-defined; temporal lobe with about 10 rather coarse punctures, not clearly differentiated into coarse and fine ones, as in *O. capito*; one temporal seta; postorbital tubercles about 0.8 as long as eye, more divergent than in *O. capito*, width across them much greater than width across eyes; eye large, round; posterior face of temporal lobe with minute pale scales which are separated from one another.

Pronotum very short, broad; length/greatest width 1.03, widest near middle; base slightly narrowed; apex more strongly narrowed; anterior part of lateral margins more oblique, less curved than in *O. capito*; margin slightly sinuate anterior to hind angle; outer carina about 0.5 as wide as inner carina at middle; outer carina narrow, convex, of nearly even width; inner carina narrowed just anterior to base, then slightly dilated; paramedian groove broader than in *O. capito*, apex of paramedian groove dilated; outer carina with about 30 fine punctures; inner carina impunctate; pronotum without setae; prosternum without precoxal carina.

Elytron rather broad, its surface microsculptured, shining, opalescent; striae not impressed, represented by rows of rather coarse, round punctures; base of Stria IV with longitudinal pollinose scarp; elytral striae without setae; metasternum nearly completely, finely punctate, but with punctures very sparse on either side of midline; female with oval lateral pits on abdominal Sternum IV; female with acute ventral tooth on anterior femur; male unknown.

This species has a broad head and divergent postorbital tubercles. It is close to *O. capito*, but differs in the shape of the pronotum, especially in having much narrower outer carinae.

O. largus will trace to *O. capito* in our key to *Omoglymmius* s. str. of New Guinea. Couplet 24' should be altered to lead to Couplet 25, which will separate the two species as follows:

- 25 (24') Outer carina slightly narrower than inner carina at middle; outer carina at anterior 0.33 broader than paramedian groove. . . . *O. capito* (Grouvelle)
 25' Outer carina about 0.5 as wide as inner carina at middle; outer carina at anterior 0.33 narrower than paramedian groove. . . . *O. largus* new species

Omoglymmius (sensu stricto) tolai new species

(Fig. 231)

Type Material.— HOLOTYPE male, labelled: "NEW BRITAIN, Rabaul, 17-VII-79 sur arbre mort, J. D. Bourne" (GVA). PARATYPE one female, mounted on same pin as male.

Description.— Length 6.7-7.2 mm. Antennal Segments I-IV coarsely punctate; Segments V-X more finely punctate; Segment XI impunctate; head distinctly longer than wide; median lobe short, oval, its tip broadly rounded; median lobe impunctate; frontal space as long as broad, nearly V-shaped, its anterior medial margin oblique, long; medial angles nearly rounded, markedly separated; posteriomedial margin curved evenly; posteriolateral margin evenly curved; occipital angle indistinct; orbital groove narrow, ended posterior to middle of eye; anterior portion of temporal lobe a convex, pollinose ridge; temporal lobe with 10-28 fine punctures; one temporal seta; postorbital, suborbital tubercles absent; eye large, round.

Pronotum rather short; length/greatest width 1.14, widest near middle; base slightly narrowed; apex markedly narrowed, margin evenly curved from middle to apex; margin scarcely sinuate anterior to hind angle; outer carina about 0.67 as wide as inner carina at middle; medial margin of outer carina sinuate just anterior to base; outer carina widest at or posterior to middle, scarcely narrowed anteriorly except at extreme apex; inner carina narrowed to base; latter truncate; outer carina with 20-38 fine punctures; inner carina with 21-23 fine punctures; pronotum without setae; prosternum without precoxal carinae.

Elytron relatively elongate, narrow; striae impressed, coarsely punctate; transverse basal scarp pollinose; base of Stria IV with longitudinal pollinose scarp; Stria IV with one seta near apex; subapical striole with one seta; Stria VII with several setae near apex; metasternum largely punctate, but with small impunctate area near middle of disc; abdominal Sterna III-VI coarsely punctate; punctures confluent near lateral margin; female with lateral pit on Sternum IV small but relatively deep, male with similar but shallower pit; both sexes with ventral tubercle on anterior femur, that of female relatively small; middle calcar small, obtuse; hind calcar triangular, proximal margin slightly concave.

This species, the first of the genus to be described from the Bismarck Archipelago, is close to several species from New Guinea. In the shape of the pronotum it comes close to *O. puncticornis* Bell and Bell. It differs from the latter species in having the punctures of the distal antennal segments markedly finer than those of the proximal segments.

The punctures of the legs and ventral surface are also notably finer than in *O. puncticornis*. *O. fringillus* Bell and Bell differs in having the temporal lobes more transverse, with the posteriomedial angles longer and more oblique, so that the most posterior points on the two lobes are separated by more than 0.5 of the greatest width of the head. The pronotum is more nearly quadrate, with the lateral margins nearly parallel except near the anterior margin. The closest species is perhaps *O. oroensis* Bell and Bell, which resembles *O. tolai* in the shape of the temporal lobes, but which has the pronotum similar to *O. fringillus*.

In our general key, *O. tolai* will trace to Couplet 20. At this point the key should be altered as follows:

4 (2')	Outer carina punctate, at least near margin	4.1
4'	Outer carina impunctate	5
4.1(4)	Median lobe concave; two medial angles, separated by shallow emargination	<i>O. insularis</i> (Grouvelle)
4.1'	Median lobe flat; one medial angle, anteriomedial margin oblique	<i>O. perplexus</i> new species

Omoglymmius (Laminoglymmius) perplexus new species
(Figs. 228, 233)

Type Material.— HOLOTYPE female, labelled: "SUMATRA, dono Grouvelle 1901, *philippensis* Chev., teste Grouvelle 1901" (GEN). The specimen was formerly mounted on the same pin as a male of *Omoglymmius (Hemiglymmius) inermis* Bell and Bell.

Description.— Length 7.1 mm. Antennal Segment XI as wide as long, apex rounded; basal setae sparse on Segments V-VI denser on VII-X; clypeus impunctate, continuous with median lobe; latter impunctate, narrow, tip pointed, not translucent; anteriomedial margin of temporal lobe almost straight, translucent area semicircular, less sharply different from remainder of temporal lobe than in *O. inaequalis*; one medial angle, latter obtusely rounded, nearly contiguous with that of opposite temporal lobe; medial angle with very narrow pollinose area; posteriomedial margin nearly rounded; temporal lobe convex, shining, with two or three coarse punctures, each with minute seta; postorbital tubercle small, about 0.5 as deep, 0.33 as long as eye, low, opposite lower 0.5 of eye; width across postorbital tubercles less than that across eye.

Pronotum relatively short, length/greatest width 1.10; widest point slightly anterior to middle; sides curved, strongly convergent to apex, latter narrow; sides oblique, slightly convergent to base, latter relatively broad; margin scarcely sinuate anterior to hind angle; paramedial groove deep, strongly narrowed anteriorly, width at middle 0.4 of that of inner carina; outer carina broad, nearly equal to inner carina at middle; outer carina with five or six punctures near lateral margin in middle 0.33; inner carina entirely impunctate; marginal groove linear.

Elytra relatively short, broad; striae shallow, intervals slightly convex, faintly microsculptured; stria punctures relatively coarse, each about 0.33 of width of interval; Stria VII with three to five setae near apex; female with shallow, semicircular lateral pit on Sternum IV; female with ventral tooth on anterior and posterior femora; male unknown.

The medial translucent area on the temporal lobe is very small and liable to be overlooked. If so, this species would be traced to Subgenus *Boreoglymmius*. In the latter species, it would be keyed to *O. lewisi* of Japan, because of the presence of a postorbital tubercle. The latter species differs in the conspicuously oblique posteriolateral margins of the temporal lobes, and in the much bigger lateral abdominal pits of the female. Also, it lacks a median gular tubercle, while *O. perplexus* has one. This appears to be a constant difference between the Subgenera *Laminoglymmius* and *Boreoglymmius*. Another superficially similar species is *O. lineatus* of southern India, in Subgenus *Indoglymmius*. The latter species lacks basal setae on the antennae, lacks a postorbital tubercle, and has a much more elongate pronotum.

With the Subgenus *Laminoglymmius*, the most similar species are *O. inaequalis* of the Andaman Islands, and *O. actae* of New Guinea. Both species have much narrower outer carinae. In addition, *O. inaequalis* has a much more conspicuous translucent area on the temporal lobe, and *O. actae* has two distinct medial angles.

O. inaequalis appears to be the species most closely related to *O. perplexus*. It appears to us that the two shared a common ancestor more recent than our hypothetical Species 3 (Part III, Diagram 2).

SUBGENUS *NAVITIA* BELL AND BELL 1978

The discovery of an additional species necessitates the substitution of a new species key.

KEY TO SPECIES (Supersedes that in Part III: 164)

- | | | |
|-------|--|---|
| 1 | Frontal grooves pollinose | 2 |
| 1' | Frontal grooves glabrous, scarcely evident | |
| | <i>O. intrusus</i> (Grouvelle) (Part III: 166) | |
| 2 (1) | Temporal lobe with eight or more punctures in addition to setiferous puncture; outer carina of pronotum with three to five punctures near base | |
| | <i>O. stylatus</i> Bell and Bell (Part III: 165) | |

- 2' Temporal lobe with one or two punctures in addition to setiferous puncture; outer carina of pronotum without punctures *O. peckorum* new species

Omoglymmius (Navitia) peckorum new species

(Fig. 230)

Type Material.— HOLOTYPE male, labelled: "FIJI: Viti Levu 1100 m., Nandarivatu Microw, 16-20 VIII - 1978 S & J Peck, Ber. Elfin for litter, rainforest, berlese litter" (BSRI). PARATYPE male, same label as holotype (BSRI).

Description.— Length 5.5 mm. Antennal stylet more elongate than in related species, about 0.3 of length of Segment XI; head cordate, slightly broader than long, temporal lobes slightly flattened; frontal grooves pollinose, broader and deeper than in *O. stylatus*; orbital groove distinct, reaching to middle of eye; head broader than in *O. stylatus*, margins slightly convergent posteriorly; temporal lobe with three coarse punctures near margin, one or two of them with temporal seta; temporal lobe otherwise impunctate.

Pronotum elongate, length/greatest width 1.23; widest anterior to middle, lateral margin distinctly sinuate anterior to hind angle; marginal groove distinct in anterior 0.67-0.75, replaced posterior by group of five widely spaced punctures; pronotal epipleuron without ventral row of punctures.

Elytra narrow, relatively elongate; last puncture of Stria III enlarged, elongate oval; striae deeper, more coarsely punctate than in related species; intervals more convex than in related species; Stria IV with complete row of five setae; one seta at apex of Stria VI; about five setae near apex of Stria VII; punctures of Sternum V not confluent laterally; male with ventral tooth on anterior femur; middle calcar obsolete; hind calcar obtuse, proximal margin obtusely angulate. Female unknown.

This species has deeper striae with coarser punctures and more convex intervals than in other members of the subgenus. The antennal stylet is larger. In other respects it shows a mixture of the characters of the previously known species. The pollinose frontal grooves give a superficial resemblance to *O. stylatus*, while the relatively short marginal groove, and the absence of punctures on the pronotal epipleuron and the outer carina are similarities to *O. intrusus*. The hind wing was checked on the paratype, and was found to be fully developed.

We dedicate this species to the collectors, Drs. S. & J. Peck.

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BOOK REVIEW

Belton, Peter. 1983. Review of mosquitoes of British Columbia. British Columbia Provincial Museum Handbook 41. 189 pp. \$5.00 Canadian.

This excellent little book describes, in simple terms, the mosquito fauna of B.C. Important information such as the biology and morphology of mosquitoes is dealt with adequately, both descriptively and diagrammatically. Simple and workable couplet keys for species identification of adult females and fourth instar larvae, are greatly aided by line drawings, habitat and species descriptions. With a little effort, the most amateur of amateurs could identify all of British Columbia's mosquitoes. The book will be an asset to any mosquito control program, where identification by inexperienced personnel is required.

Introductory sections add interest to the book. The description of the Life Zones of B.C. shows the great diversity of British Columbia's terrain – from rain forest, tidal pools and salt marshes in the west to arid regions in the east, and from arctic and subalpine zones in the north to more temperate ones in the south. With this great climatic and geographic diversity goes a concomitant diversity in the mosquito fauna. Sections about mosquitoes in the culture of The Northwest Coast Indians, the collection and preservation of mosquitoes, and the history of mosquito study and management in B.C. are included, as well as a useful glossary and reference section.

Because the species composition of B.C. is very similar to that of Alberta, the key could be used in Alberta. A total of 46 species in 5 genera occur in B.C. – 33 *Aedes*, 3 *Anopheles*, 3 *Culex*, 6 *Culiseta* and 1 *Mansonia*. In Alberta, 42 species occur in the same 5 genera. Five species occur in Alberta but are absent from the species record of B.C., namely, *Aedes churchillensis*, *Ae. decticus*, *Ae. nigromaculis*, *Ae. schizopinax* and *Culex restuans*. Of these five Dr. Belton has included *Ae. nigromaculis* and *Ae. schizopinax* in the couplet key. The other three species are rare in Alberta and should not prove a problem. The existence of regional morphological variations should be kept in mind, however, when using the key.

I have only two criticisms, firstly the book binding will not survive the great deal of use that such a key will receive; a ring binding would have been more serviceable. And secondly, there is no key to male identification. Although the author does point out that males can be keyed using Carpenter and La Casse, this key is now somewhat out of date. Male identification is somewhat easier, but requires slide preparation in most cases and the use of a compound microscope.

The publication of this book by the British Columbia Provincial Museum is the fortyfirst in what is already an excellent series. I anticipate that Peter Belton has started something that will result in others writing similar pocket books on their local mosquito fauna.

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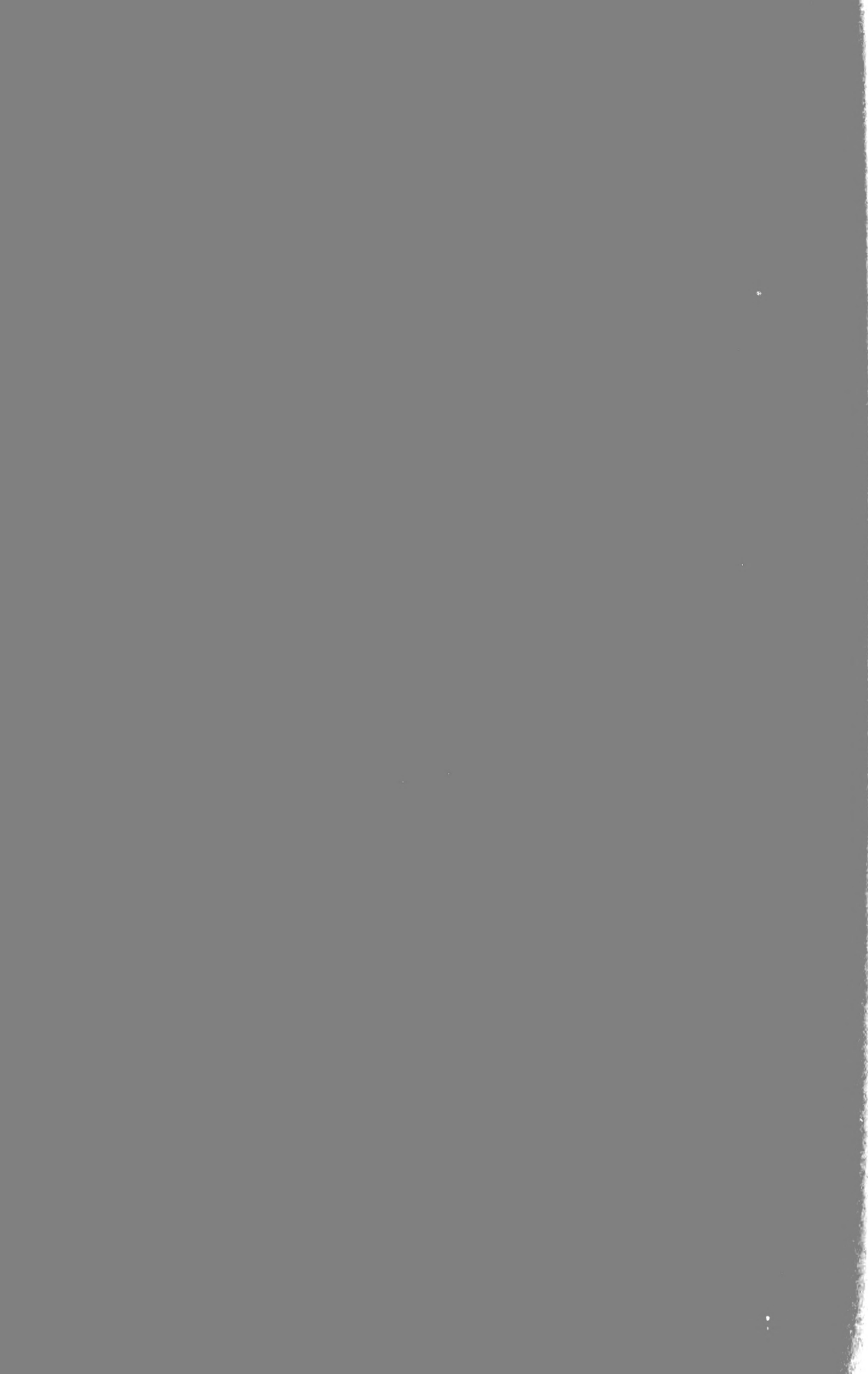
BOOK NOTICE

Griffiths, G.C.D. (Editor). Flies of the Nearctic Region. E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller) Stuttgart. Volume VIII. Cyclorrhapha II (Schizophora: Calyptratae) Part 2, Number 2. Anthomyiidae, by G.C. Griffiths, pp. 161–288 (1983). \$56.76 US. Part 2, Number 3. Anthomyiidae, same author, pp. 289–408 (1984). \$56.76 US.

G.E. Ball reviewed earlier issues of this series in *Quaestiones Entomologicae* (1980, 16(3/4): 676–678; 1983, 19(3/4): 489–490), including Part 1 of Griffiths' treatment of the nearctic species of Anthomyiidae. That part contained a brief introduction to the family, a thorough taxonomic treatment of the genus *Pegomya* Robineau-Desvoidy subgenus *Pegomya* and ended mid sentence in his description of *P. magdalensis* new species. Part 2 concludes his consideration of the subgenus *Pegomya*, begins that of the subgenus *Phorea* and ends mid sentence in a description of *P. valmariensis* new species.

In Part 3, Griffiths finishes with *Pegomya* and provides separate keys for the identification of males (pp. 337–346) and females (pp. 346–351), thus rectifying one of the weaknesses of Part 1 noted by Ball (*Quaest. Ent.* 19: 490). In addition, this fascicle contains full taxonomic consideration of the species of *Emmesomyia* Malloch and *Parapegomyia* new genus, including keys to species and a "first reference list" of papers cited in Parts 1 – 3 and expected to be cited in forthcoming parts. Thus, Griffiths' finished treatment of the family will be unusual in having its list of references in the middle rather than at the end. All Ball's critical comments about Part 1 apply equally to Parts 2 and 3.

B.S. Heming
Department of Entomology
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Entomologicae

A periodical record of entomological investigations,
published at the Department of Entomology,
University of Alberta, Edmonton, Canada.

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SOME ECONOMIC EFFECTS OF OUTBREAKS OF BLACK FLIES (*SIMULIUM LUGGERI* NICHOLSON AND MICKEL) IN SASKATCHEWAN¹

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Quaestiones Entomologicae

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ABSTRACT

Larvae of Simulium luggeri Nicholson and Mickel were first detected in the South Saskatchewan River in 1968, coincidental with appearances of aquatic weeds. They became abundant in both the South and North branches in Saskatchewan by 1971. Damaging outbreaks occurred for the following reasons: larvae readily drifted downriver and colonized extensive beds of weeds, S. luggeri is multivoltine, adults dispersed widely and attacked most mammals including people, swarming about heads causing stress and hyperactivity. During outbreaks, grazing and breeding activities of livestock were interrupted and lactation reduced. Increased incidence of stress-related injuries and diseases including broken limbs, keratitis, mastitis, calfhood scours and pneumonia occurred.

Chronic outbreaks of S. luggeri have occurred every summer since 1975 in east-central Saskatchewan. Use of methoxychlor larvicide reduced potential severity of many outbreaks. The most destructive outbreaks occurred in 1978 when black flies spread onto about 38,000 km² of east-central Saskatchewan and caused measurable economic losses in about 5,700 km². Losses to beef producers in 1978 were estimated to have exceeded \$2.9 million and included unrealized weight gains, delayed conceptions, fatalities, replacement of debilitated bulls and increased costs for labour, veterinarians' services, fence repairs and supplementary feeding. Losses to dairy producers were estimated to have exceeded \$57,000. Milk production from severely affected cows did not return to normal until after new lactation cycles commenced, sometimes several months after outbreaks ceased in the fall.

Producers responded in several ways, for example by changing management practices, by reducing or eliminating herds, by converting pasture lands to less productive uses, and by submitting petitions to governments for improved control of larvae.

RÉSUMÉ

En 1968, la mouche noire, Simulium luggeri Nicholson & Mickel, commençait à se reproduire dans la rivière Saskatchewan. L'apparition de S. luggeri a coïncidé avec l'envahissement de la rivière par la flore aquatique. Selon l'auteur, des attaques sévères de mouche noire se sont produites pour les raisons suivantes: les larves sont aisément entraînées par le courant et s'attachent aux vastes bancs de plantes aquatiques; la mouche noire est plurivoltine; les insectes adultes sont capables de coloniser de vastes superficies et ils s'attaquent à la plupart des mammifères, y compris l'homme; les insectes ont tendance à s'attaquer à la tête des animaux, causant chez ceux-ci des signes de stress et d'hyperactivité. Au cours des attaques de mouche noire, on a observé que les animaux cessaient de brouter et de se reproduire et que les vaches en lactation produisaient moins de lait. On a aussi noté un nombre accru de blessures et de maladies causées par le stress, telles que membres rompus, kératite, mastite, diarrhée du veau et pneumonie.

¹Contribution No. 866 of the Research Station, Saskatoon

Les attaques de mouche noire se sont produites de façon chronique chaque été depuis 1975 dans la région centre-est de la Saskatchewan. L'emploi du larvicide méthoxychlor a contribué à réduire la sévérité de plusieurs attaques. Les attaques les plus sévères se sont produites en 1978, les mouches noires infestant près de 38 000 km² et causant des dommages mesurables sur près de 5 700 km². En 1978, les pertes subies par les producteurs de boeuf de boucherie ont été estimées à plus de 2.9 millions de dollars. Ces pertes ont résulté des faits suivants: gains de poids plus lents, conceptions retardées, pertes d'animaux, ainsi que coûts de remplacement des taureaux malades, de la main d'oeuvre supplémentaire, des soins vétérinaires, des réparations aux clôtures et des suppléments alimentaires. Par ailleurs, les producteurs laitiers ont subi des pertes estimées à plus de 57 000 \$. Il fut observé que le rendement des vaches laitières sérieusement atteintes ne redevenait normal qu'après le début d'un nouveau cycle de lactation, qui ne survenait parfois que plusieurs mois après la disparition des mouches noires, en automne. Les producteurs ont combattu la mouche noire de différentes façons: en modifiant leurs méthodes de gestion, en réduisant ou en éliminant complètement les troupeaux, en utilisant les pâturages à des fins moins productives, ou en pétitionnant pour l'amélioration du contrôle des larves.

INTRODUCTION

Every summer since widespread outbreaks of the black fly *Simulium luggeri* Nicholson and Mickel commenced in 1976 in east-central Saskatchewan, residents have demanded government assistance with abatement. Methoxychlor larvicide is effective (Fredeen, 1974, 1975) and its use in the Saskatchewan River apparently is not permanently harmful to non-simuliid fauna (Fredeen, 1983). However, use of larvicide cannot be condoned without unequivocal proof of need. The purpose of this paper is to compile and assess evidence of losses to beef and dairy cattle producers in Saskatchewan resulting from outbreaks of *S. luggeri*.

Populations of black fly larvae in both branches of the Saskatchewan River in Saskatchewan were dominated by *S. arcticum* until the mid-1970's. From this river sporadic outbreaks of *S. arcticum* spread widely into surrounding farmlands killing numerous animals (Rempel and Arnason, 1947; Fredeen, 1958). Major outbreaks of *S. arcticum* ceased in 1948 with the advent of chemical larviciding (Fredeen, 1953, 1977(a)) but minor outbreaks continued because of downstream drift of eggs and larvae from untreated sections.

In early years, the Saskatchewan river usually was deep and turbid throughout much of the ice-free season with beds of sand and rocks completely free of vegetation. In 1968, completion of a hydroelectric dam on the South Saskatchewan River, 115 km south of Saskatoon (about 350 km above its confluence with the North Saskatchewan River) (Fig. 1) created a reservoir 250 km long, a complete barrier to further migration of larvae down that river (Fredeen, 1977(b)). By 1971 the South Saskatchewan River below the reservoir had become relatively shallow during ice-free months due to storage of water for wintertime generation of hydropower (Fig. 2, S.S.R.). The reservoir served as a sink for suspended solids, and the combination of shallow, clear water in the river below the dam allowed sufficient insolation to encourage, for the first time, growth of massive beds of algae¹ and broad-leaved plants² on the river bed. Growths of aquatic plants undoubtedly also were enhanced by nutrients released from urban and rural communities. This is evident today when comparing growths above and below large cities on the Saskatchewan River.

In 1975 similar trends became evident in the North Saskatchewan River (Fig. 2, N.S.R.). Relatively shallow, clear water replaced the large, turbid summertime volumes of previous years. This was due in part to drought conditions which greatly reduced runoff in a major

¹Mainly *Cladophora glomerata* (L.) Kutzling

²The four most common species are *Ceratophyllum demersum* L., *Myriophyllum exalbescens* Fernald, *Potamogeton crispus* L., *P. pectinatus* L.

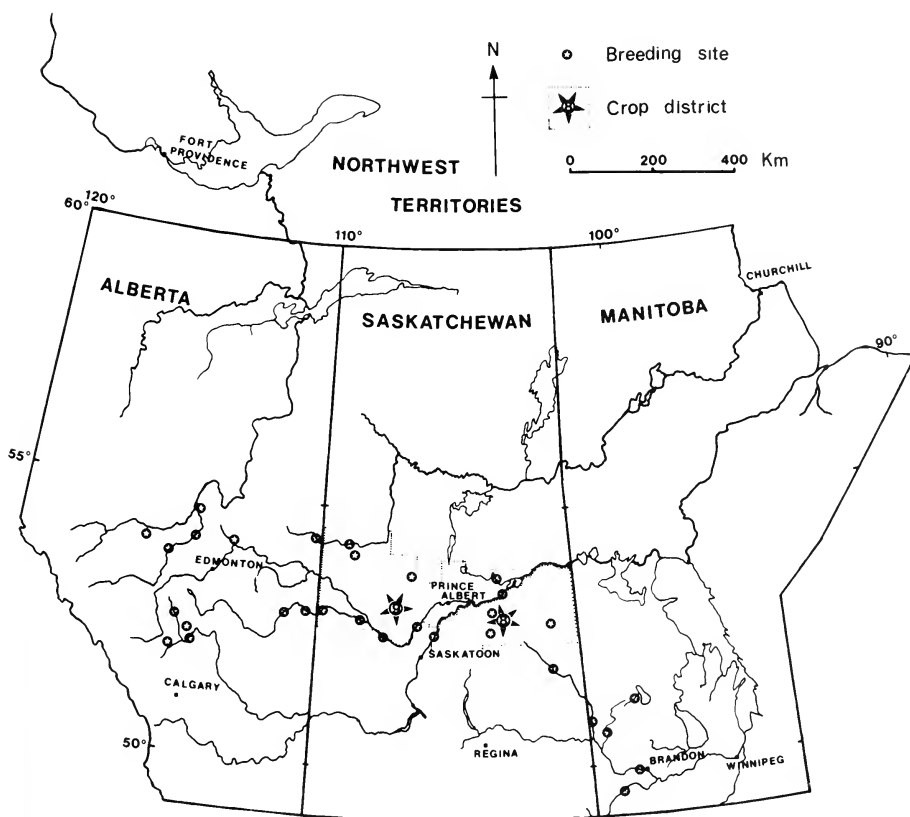


Fig. 1. Map of Alberta, Saskatchewan and Manitoba indicating sites where immature stages of *Simulium luggeri* were collected from the Saskatchewan River in southern Saskatchewan and Alberta, and from other river systems. The boundaries of Crop Districts 8 and 9 outline regions in Saskatchewan where most outbreaks occurred in recent years.

portion of that watershed, and in part to completion of two hydroelectric reservoirs in the foothills, Brazeau in 1962 and Abraham Lake in 1972. Together they controlled about half of the volume of water reaching the lower end of the North Saskatchewan River. Extensive summertime beds of algae and aquatic broad-leaved plants appeared, especially between Edmonton, Alberta and North Battleford, Saskatchewan. Paterson and Nursall (1975) suggested that the presence of algae below Edmonton was the result of increased nutrient content (chiefly nitrates) in that portion of the river. Weed beds above North Battleford are occupied mainly with larvae of *S. vittatum* Zetterstedt, a species relatively tolerant of organic pollution.

These environmental changes in both branches of the Saskatchewan River discouraged accumulation and development of larvae of *S. arcticum* which prefer to attach to clean boulders in fast-flowing water, but encouraged invasions of *S. luggeri*, *S. vittatum*, *S. meridionale* Riley,

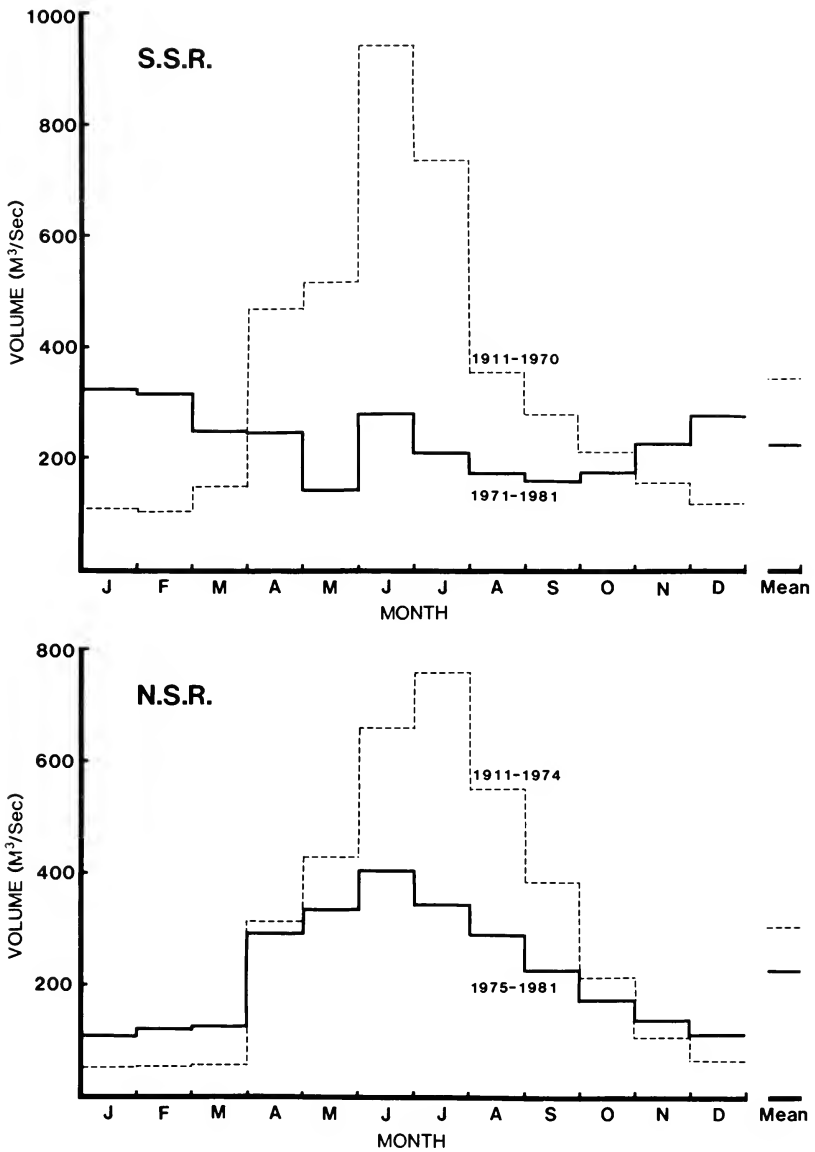


Fig. 2. Average monthly volume flows in the Saskatchewan River: S.S.R. = South Saskatchewan River at Saskatoon, 1911 through 1970, and 1971 through 1981; N.S.R. = North Saskatchewan River 1911 through 1974, and 1975 through 1981 (Environment Canada 1980 (a), 1981, 1982).

TABLE 1. MAXIMUM DENSITIES OF LARVAE AND PUPAE OF FOUR SPECIES OF BLACK FLIES OBSERVED ON NATURAL AND ARTIFICIAL SUBSTRATES IN THE NORTH AND SOUTH SASKATCHEWAN RIVERS IN SASKATCHEWAN (NUMBER/CM²)

	North Saskatchewan River near Prince Albert, Sask.				South Saskatchewan River near Birch Hills, Sask.			
	<i>S. arcticum</i>	<i>S. luggeri</i>	<i>S. meridionale</i>	<i>S. vittatum</i>	<i>S. arcticum</i>	<i>S. luggeri</i>	<i>S. meridionale</i>	<i>S. vittatum</i>
1947 to								
1968	100+	<1	<1	<1	100+	<1*	<1	<1
1969	8	0	<1	<1	8	<1	<1	3
1970	91	<1	<1	<1	—	—	—	—
1971	49	3	<1	<1	—	—	—	—
1972	36	6	<1	<1	—	—	—	—
1973	34	1	<1	18	—	—	—	—
1974	3	<1	<1	<1	—	—	—	—
1975	35	10	<1	<1	—	—	—	—
1976	12	32	<1	1	—	—	—	—
1977	13	128	<1	20	3	37	<1	16
1978	2	65	2	13	3	61	<1	15
1979	2	70	6	316	1	12	<1	6
1980	4	98	9	370	1	17	<1	20
1981	9	64	26	469	1	30	<1	52

*In the South Saskatchewan River larvae of *S. luggeri* were first detected in 1968.

and other species which prefer to attach to leaves of aquatic plants (Fredeen, 1981).

RECENT TRENDS IN SPECIES OF BLACK FLIES INHABITING THE SASKATCHEWAN RIVER IN SASKATCHEWAN

Methods

Annual trends in maximum densities of larvae of the four main species of black flies inhabiting the north and south branches of the Saskatchewan River in Saskatchewan are shown in Table 1. Until 1969, populations of larvae were estimated by counting numbers attached to rocks collected from rapids. In 1969 accuracy of estimates presumably was improved when we began to anchor artificial substrates for larvae to attach to (metre-length pieces of rope) (Fredeen and Spurr, 1978). Between 1969 and 1976 larvae were counted at weekly intervals for only a few weeks in late spring each year or until chances of outbreaks of *S. arcticum* were considered to have ended for the year (*S. arcticum* generally peaked in May or June). But beginning in 1977, weekly samples were collected throughout each summer from both branches of the Saskatchewan River because the newly-established *S. luggeri* was multivoltine and larvae were abundant and had to be monitored throughout much of the ice-free season.

South Saskatchewan River

Populations of larvae in the South Saskatchewan River were dominated by *S. arcticum* each spring until about 1977 (Table 1). The final major outbreak of *S. arcticum* believed to have originated at least in part from the South Saskatchewan River, occurred June 13 to 18, 1967. In that outbreak 43 animals were known to have been killed in communities extending southeastwards more than 100 km from Prince Albert.

Larvae of *S. luggeri* (indicating a breeding population) were first collected from the South Saskatchewan River in July and August, 1968. But it was not until 1977 that we commenced regular weekly collections from that river and these showed that *S. luggeri* had replaced *S. arcticum* as the dominant species. Previously, I had found it breeding only in small, weedy rivers across Manitoba, Saskatchewan and Alberta (Fig. 1). Shewell (1958) reported it from the Churchill River on Hudson Bay and from the Mackenzie River and tributaries as far north as Norman Wells, N.W.T. The earliest observed outbreak of *S. luggeri*, believed to have originated from the South Saskatchewan River, occurred on August 22, 1972 when this species was identified in swarms causing cattle to run. Since then outbreaks of varying severity have originated from the final 150 km of this river every year.

North Saskatchewan River

The final recorded outbreak of *S. arcticum* of economic proportions from the North Saskatchewan River occurred in mid-June 1972. During that outbreak at least 19 cattle were killed near a section of that river upstream from Prince Albert.

In 1971 and 1972, during tests of artificial substrates, there were significant increases in numbers of larvae of *S. luggeri* in samples collected in late summer from several sites in the North Saskatchewan River indicating establishment of a breeding population in that river. Previously, larvae had been collected from the North Saskatchewan River only from restricted sites below the mouths of small tributaries.

In May through October 1975, the volume of the North Saskatchewan was greatly reduced (to about 50 percent of long-term means) and coincidentally by early June, larvae of *S. luggeri* became unusually abundant. In May, 1976 its larvae outnumbered those of *S. arcticum* in the

North Saskatchewan for the first time (Table 1) and within a month the first widespread outbreaks of *S. luggeri* began from that river. Since then, larvae of *S. luggeri* have remained relatively abundant, especially in the final 300 km of the North Saskatchewan River before its confluence with the south branch, and in the entire 130 km of the main Saskatchewan River between the confluence and Tobin Lake at Nipawin (Fig. 1). Although numbers of larvae of *S. vittatum* began to surpass those of *S. luggeri* by 1979 (Table 1), significant outbreaks of that species have not been reported yet, perhaps because livestock appear to be relatively tolerant of it. Larvae of *S. arcticum* still occur regularly although in small numbers every year in both branches of the Saskatchewan River, indicating potential for staging a comeback should conditions change in its favor.

CHRONOLOGY OF OUTBREAKS OF *S. LUGGERI* FROM THE SASKATCHEWAN RIVER

1976

In 1976, larvae of *S. luggeri* accumulated on artificial substrates (rope pieces) anchored in the North Saskatchewan River in rapids 22 km below Prince Albert, Saskatchewan at an average rate of 1550 larvae per metre of rope per week during May and June. A maximum density of 32 larvae per cm² of substrate surface (Table 1) was observed on June 22. Populations were not measured in the South Saskatchewan River that year. Although the maximum density observed in the North Saskatchewan was three times larger than that observed in 1975 there were no concerns about possibilities of damaging outbreaks because *S. luggeri* had not been known to lethally poison animals as did its predecessor, *S. arcticum*. Also there had been no complaints of black fly attacks on livestock in 1975, although a year or more later some producers did recall that their cattle had been noticeably bothered by black flies in 1975.

Environmental changes in 1976 that may have accounted, at least in part, for observed increases in numbers of larvae included greatly reduced river volumes and higher water temperatures. Ice on the North Saskatchewan River broke up a week earlier than normal that spring, and water volumes in both branches remained much below normal throughout May, June and July. Also mean daily air temperatures in May were 17 percent above normal and hours of sunshine 32 percent above normal. For all of these reasons, river water in both branches of the Saskatchewan River warmed up more rapidly than normal that spring, attaining daily maxima of 20°C 3 to 4 weeks earlier than in previous years. Also, because relatively low water levels and low water turbidities had allowed greatly increased insolation, growths of aquatic weeds (favored attachment sites for larvae of *S. luggeri*) and planktonic algae (which served as food) were increased.

During ice-free months in earlier years, water turbidities as high as 7270 mg/L were reported for the South Saskatchewan River and 3050 mg/L for the North Saskatchewan (Environment Canada, 1980 (b)). Microscopic examination of turbid water showed phytoplankters to be very scarce but numbers were not recorded.

In 1976, weekly measurements of turbidity indicated summertime maxima of only 52 mg/L for the south branch at Birch Hills and 99 mg/L for the north branch near Prince Albert. Phytoplankters were so abundant that the water was greenish, but numbers were not counted. In 1978, under similar turbidity conditions (maxima of only 97 mg/L for the south branch and 211 for the north), maxima of 550 and 1100 phytoplankters per 0.001 mL of river water were recorded for these two branches.

Weather conditions, especially air temperatures, also generally favored black fly attacks on animals. Attacks by *S. luggeri* are most vigorous between about 20 and 25° C, and daily maximum temperatures above 20° C were recorded on 21 days in May, 19 in June, 28 in July and 28 in August.

In 1976, pupae of *S. luggeri* were first collected on May 25. The first report of outbreaks in 1976 came from Mr. Glen Love, who had a mixed farm between the north and south branches of the Saskatchewan River about 30 km east of Prince Albert. He first observed black flies around his cattle on the afternoon of May 29. From then on until June 8 his livestock were so severely attacked when outside during daylight hours that they had to be fed and watered indoors. Mr. Love marketed most of his cattle on June 8 to avoid further costs of supplementary food and labour. Black fly swarms at that time consisted of 98 percent *S. luggeri* with about 2 percent *S. arcticum*, *S. meridionale* and *S. vittatum*.

During that first week of June, livestock throughout a 7,000 km² area, extending some 30 km on either side of the entire Saskatchewan River between Prince Albert and Nipawin (Fig. 3), were severely attacked by *S. luggeri* every day. Producers claimed that their cattle were continually surrounded by clouds of black flies during daylight hours and that attacks were especially severe before thunderstorms on June 3 and 4. Smudges were kept burning throughout the region, even in the largest community pastures. There were numerous complaints from people who claimed they also were bitten. Even with repellents, black flies swarmed around them so thickly that they could not avoid breathing them in.

Cooler weather (daily maxima of 13 to 20°C) on 11 days between June 8 and 26 was believed responsible for several lulls in outbreaks. There was also a decline in numbers of larvae in the river until after second generation larvae appeared in June. However, between June 26 and July 15 swarms of *S. luggeri* again severely affected livestock and people in widespread areas, including an additional 10,000 km² of rural and urban lands to the south, and 6,000 km² of recreational lands to the north, extending almost as far north as La Ronge (Fig. 3). This second series of outbreaks declined noticeably by mid-July, apparently due in part to a single injection of methoxychlor larvicide into the North Saskatchewan River on July 7.

A third series of widespread outbreaks in 1976 occurred throughout most of August and September and lasted until warm weather ended in the fall.

In summary, residents in some 23,000 km² of agricultural and recreational areas in Saskatchewan complained in 1976 of black fly outbreaks, by telephone calls and letters to federal and provincial offices in at least ten centres. Complaints of damage to livestock came from producers from diverse regions totalling about 2,500 km². There were three major periods of attack, probably related in part to production of at least three generations of *S. luggeri*. Ninety-five to 99 percent of the black flies in attacking swarms were *S. luggeri*. The remainder were *S. arcticum*, *S. meridionale* and *S. vittatum* as indicated by sweep net collections.

1977

The larval monitoring program was greatly enlarged in 1977 with artificial substrates (rope pieces) anchored and exchanged weekly in six sites, May through August. Comparisons of rates of accumulation of larvae with rates in 1976 were possible only for May and June, and only for one site located in rapids 22 km below Prince Albert on the North Saskatchewan River. There, larvae accumulated at an average rate of 7,000 larvae per metre of rope per week through May and June and 7,180 for May through August. This indicated an unusually large, persistent drift of larvae downstream into the larvicide-treated section of the river throughout the summer. The

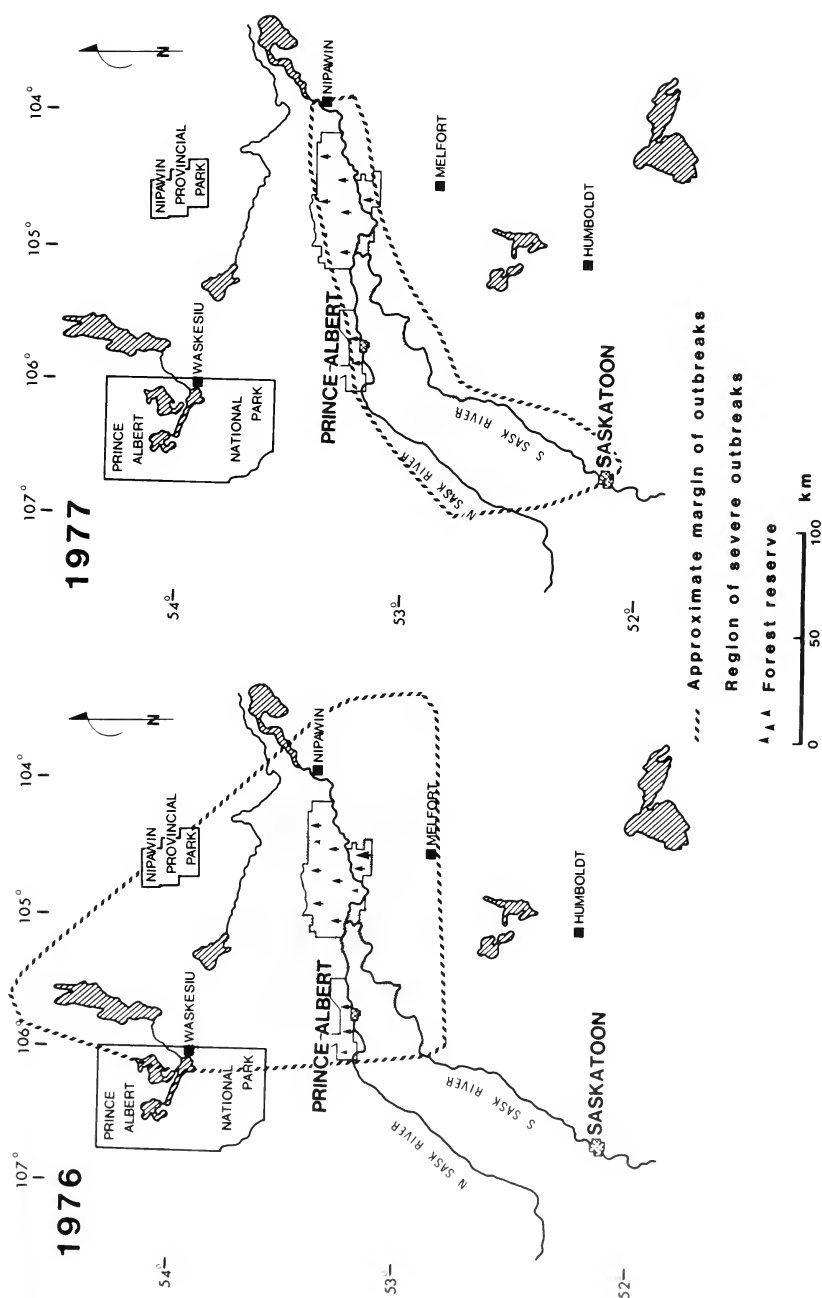


Fig. 3. Maps of central Saskatchewan showing approximate areas subjected to outbreaks of *Simulium luggeri* in 1976 and 1977, and specific localities from which most complaints of damage were received.

May-June rate was about 4.5 times larger than for the same period in 1976. A maximum density of 128 larvae/cm² of substrate surface occurred on May 10 (Table 1).

Each of the north and south branches of the Saskatchewan River was injected at one site with methoxychlor larvicide on each of three dates in 1977 (Fredeen, 1983). Treated sites were rapidly repopulated that summer. For example, following injections on July 4, numbers of larvae on artificial substrates 42 km downstream in the south branch initially declined by 78 percent but returned to pre-treatment levels within seven days. In the north branch 61 km downstream from the injection point in that river, numbers of larvae initially declined by 85 percent but a week later were 2.4 times larger than before treatment! In the main Saskatchewan River, an additional 71 km downstream from those monitored sites, numbers of larvae on artificial substrates declined by 75 to 95 percent following each injection, but within three weeks exceeded pre-treatment numbers.

Attacks on livestock commenced during the last week of May, but practically ceased by June 3. They recommenced June 29 and continued sporadically throughout the remainder of the summer whenever the weather was suitably warm. The total area where black flies were seen included some 6,000 km², generally within 10 to 15 km of either branch of the Saskatchewan River (Fig. 3). Severe outbreaks were reported from about 400 km² of farmlands.

1978

The worst outbreaks of *S. luggeri* on record occurred in 1978. In May through August, a mean density of 3180 larvae attaching weekly to metre-length rope-piece substrates anchored in the North Saskatchewan River indicated a high rate of drift of larvae downstream into treated sections of that river. Larvicide was injected three times into the North Saskatchewan River, all at Prince Albert, 25 km above the monitoring site. (This was unlike the previous year when only one of the injections was made above the monitoring site.) Four days after the first injection on May 26, numbers of larvae attached to artificial substrates had declined by 77 percent. Seven days later numbers were still 48 percent lower than before the injection. However, an unusually high rate of downriver drift of larvae following the second injection on June 20 caused a 2.9 fold increase in density, rather than the expected decrease within one week. Two weeks after that injection, density had increased even more, to 3.8 fold that seen before the injection. One week after the third and final injection on August 8, numbers of larvae had declined by 62 percent and two weeks afterwards, were still 48 percent lower than before the injection.

In the South Saskatchewan River mean weekly numbers, May through August, increased from 1,400 in 1977 to 3,340 in 1978. This occurred despite four larvicide injections 32 km above the monitoring site. The first injection, May 26, was considered successful and caused an 84 percent reduction in numbers of larvae during the first week and a further decline to 95 percent by the end of the second week. The second injection, June 20, was not successful because within one week, numbers of larvae had increased by 1.4 fold pre-treatment values and by the end of the second week, by 3.1 fold. One week after the third injection, on July 21, numbers of larvae had declined by 70 percent but, by the end of the second week, numbers had increased by a factor of 5.3 over those seen before the injection. Reductions of 69 and 76 percent were observed after the fourth injection on August 8, perhaps not so much because of that injection, but because of the normal seasonal decline at that time of the year.

In the main Saskatchewan River 70 km downriver from the confluence of the two branches, mean densities of larvae attaching weekly to artificial substrates May through August increased from 275 per week in 1977 to 1,600 per week in 1978. Drift of larvae out of the branches following larvicide injections was responsible for much of this increase. Although numbers declined by 51 percent following the first injections into both branches on May 26, they increased six-fold following the second pair of injections on June 20 and 65-fold after the third injections (south branch only) on July 21! After the fourth and final pair of injections on August 8, numbers declined by 99 percent but this decline may have been due partly to a normal seasonal trend not related to larviciding. Results in general indicated, as in previous years, that injections of larvicide into the two branches of the river could not guarantee reductions in the main river below the confluence, but that dangerous increases might occur instead, especially during June and July.

Casual observations at sites additional to the three regular monitoring sites in 1978 indicated that each larvicide injection did reduce numbers of larvae in at least a portion of the river. However, in general, these treatments failed to prevent massive outbreaks for at least three reasons: 1) The first injections were made at least 1 week too late, delayed until May 26 because of a lengthy hatching period of overwintered eggs that year. This was a mistake, because, by that date, adults of *S. luggeri* had already commenced emerging. These eventually laid sufficient eggs to allow production of massive numbers of second-generation larvae. 2) The weedy South Saskatchewan River should have been injected at several sites on each date instead of at only one. 3) The main Saskatchewan River downstream from the confluence of the two branches also should have been injected in June, July and August. By May 26 adults of *S. luggeri* already were causing cattle to stampede in pastures eastward from Prince Albert, mainly along the South Saskatchewan River. By May 31 many herds in more than 5,000 km² of farmlands between Prince Albert and Nipawin (Fig. 4) were reported to be under very severe attack, and by June 3 black flies had moved north, against prevailing winds, through some 20 km of dense woodlands in the uninhabited Nisbet Forest from the main Saskatchewan River, to commence what was to be about 16 weeks of continuous harassment of people and livestock in the Smeaton, Choiceland, and White Fox areas. Six days of northerly winds in late May and early June also carried dense swarms southward, and by June 3 reports of severe black fly problems were coming from as far south as Wynyard, some 170 km south of the nearest point of emergence on the Saskatchewan River. Strong easterly winds on June 5, 6, 9, 10, 12 and 13 then carried many of these black flies even further, to more than 40 km southwest of Saskatoon (Fig. 4). These black flies apparently had travelled more than 300 km from their origin.

In summary, livestock and people in an area probably exceeding 38,000 km² were affected by black flies in 1978. Almost one-seventh of this area, about 5,700 km², was subjected repeatedly to very severe attacks until after a second set of larvicide treatments on June 20, and sporadically thereafter until late September. Outbreaks in 1978 were more severe and widespread than in any year since outbreaks commenced in 1972.

1979

Minor outbreaks of relatively short duration occurred throughout an 18,000 km² area in central Saskatchewan in 1979 (Fig. 4). Black flies were reported mainly from areas adjacent to, and between, the two branches of the Saskatchewan River. Severe outbreaks were reported from areas totalling only about 750 km², immediately adjacent to the Saskatchewan River between Prince Albert and Nipawin.

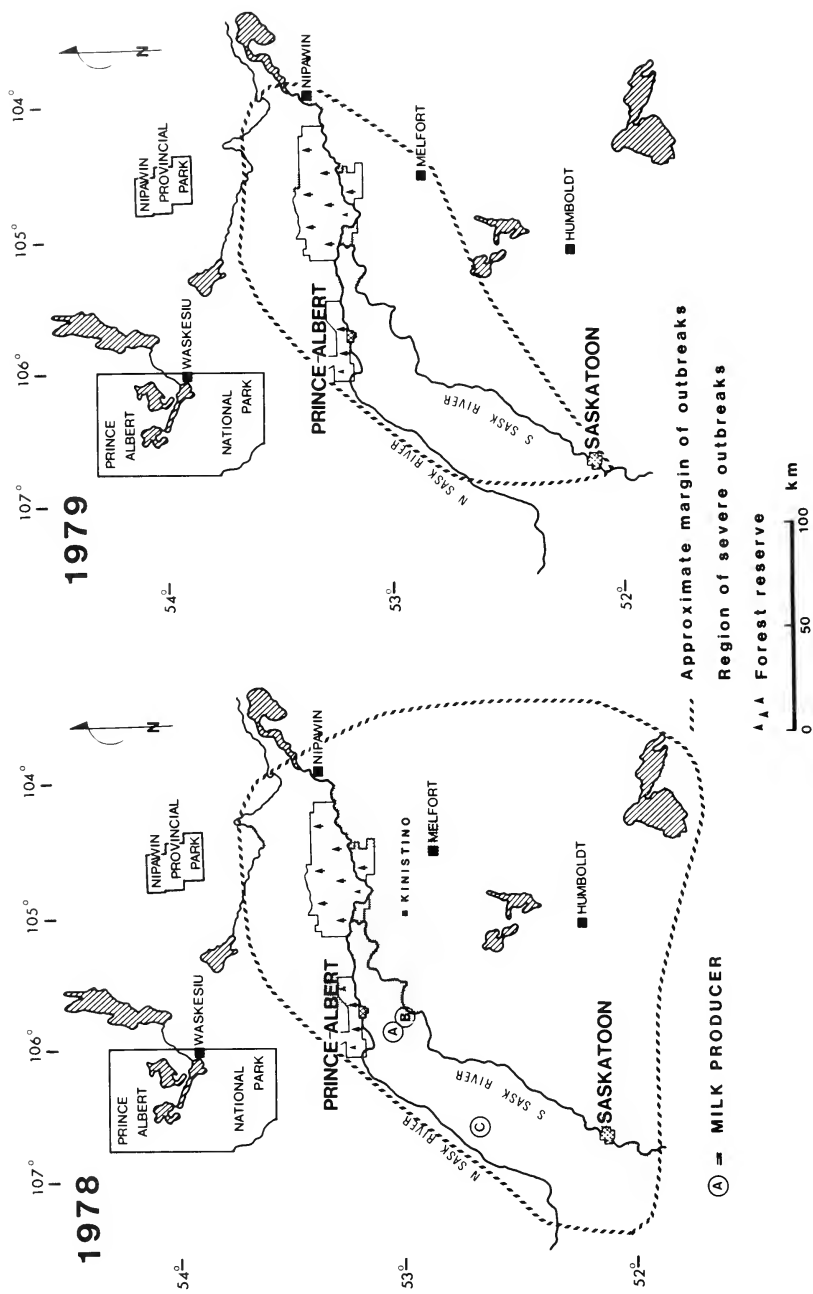


Fig. 4. Maps of outbreaks in 1978 and 1979.

Numbers of larvae accumulating weekly May through August on metre-length rope pieces anchored in the North Saskatchewan River averaged 3,340, numbers similar to those seen in 1978. However, few larvae were allowed to pupate because of five timely injections (one in two locations) of methoxychlor larvicide. Mean densities of larvae in the South Saskatchewan River were only about one-tenth those seen in 1978 due not only to three timely injections of larvicide but also to the use of several injection sites in this weedy river.

For the first time, the main Saskatchewan River below the confluence was injected. Four consecutive injections (one in two sites) prevented most larvae which may have drifted downriver from the two branches from maturing.

Livestock producers were particularly satisfied with results of the larval abatement program in 1979 and petitioned federal and provincial governments that the program be continued in future years.

1980

In 1980 outbreaks again were relatively minor and although black flies were reported at one time or another from about 20,000 km², severe outbreaks occurred in only about 400 km², mainly near the rivers as in 1979 (Fig. 5).

Densities of larvae in both branches of the river were unusually high in May but timely treatments with larvicide prevented many from maturing. Mean numbers from May through August were similar to those observed in 1979: 3,310 larvae per metre of rope in the north branch and 540 in the south. Larvicide was injected only once, on May 16 into the north branch and twice, at two locations each time into the south branch. The main river below the confluence was not injected because populations of larvae remained very low there all summer.

1981

Outbreaks were less troublesome in 1981 than in 1980 with black flies being reported from only about 7,400 km² (Fig. 5).

Mean weekly numbers of larvae of *S. luggeri* declined from those seen in 1980 to 1,570 per metre of rope in the north branch, but increased slightly to 670 in the south branch. Larvicide was injected four times into the north branch, three times into the south branch and once below the confluence of the branches.

FACTORS CONTRIBUTING TO DAMAGING OUTBREAKS OF *S. LUGGERI*

My first experience with an outbreak of *S. luggeri* occurred on August 6 and 7, 1951 when I observed horses stampeding under attack from black flies that were emerging from the relatively small Battle River about 20 km west of North Battleford, Saskatchewan. Numbers of black flies (all *S. luggeri*) were relatively small and effects were negligible. This species had been named only the previous year by Nicholson and Mickel (1950) from specimens collected in Minnesota and Wisconsin. The authors believed at that time that *S. luggeri* was occasionally bothersome to horses but not to people.

As long as *S. luggeri* was restricted to breeding in small prairie rivers, potential for creating damaging outbreaks was limited. But when it commenced breeding in the Saskatchewan River, potential with regard to intensity, duration and areas affected increased manyfold. At first there seemed no reason for concern because larvae became abundant only in late summer, and numbers waned quickly with advent of cooler temperatures in August and September.

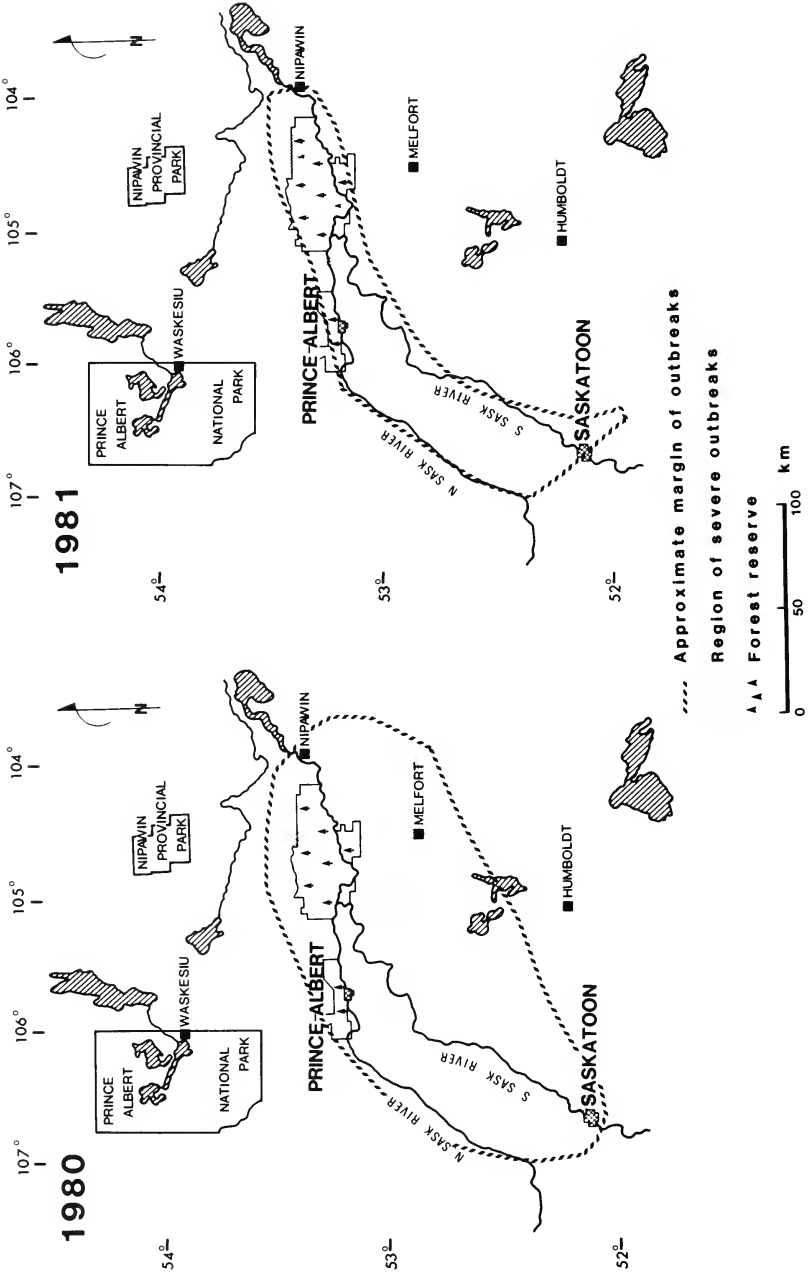


Fig. 5. Maps of outbreaks in 1980 and 1981.

Furthermore, during occasional brief outbreaks no animals were killed as had happened frequently with *S. arcticum*.

It was not until 1976 that the first summer-long outbreaks of *S. luggeri* from the Saskatchewan River occurred. Those outbreaks became so severe by mid-summer that larviciding was initiated using strategies initially developed to prevent outbreaks of *S. arcticum* (Fredeen, 1974, 1975). But whereas an outbreak of *S. arcticum* usually could be prevented with a single injection of methoxychlor larvicide into the Saskatchewan River, such a treatment proved relatively ineffective against *S. luggeri*. Research in subsequent years indicated several reasons why outbreaks of *S. luggeri* of economic proportions developed, and why major failures occurred in a larviciding program that had been used successfully against *S. arcticum*.

Major outbreaks occurred because:

1. Immense numbers of larvae of *S. luggeri* were capable of inhabiting weed beds in the Saskatchewan River, and since the species was multivoltine, numbers tended to increase during succeeding generations May through August each summer, sometimes in spite of larvicide treatments. Enormous numbers of larvae frequently drifted downriver from untreated sections for natural reasons still under investigation.

2. Adults were capable of dispersing great distances on the wind. The Saskatchewan River had the potential for producing such enormous numbers of black flies that even long-distance movements did not disperse the black flies too thinly to prevent them from disturbing livestock. In 1978 *S. luggeri* drifted on northerly winds and created problems as far away as Wynyard, some 170 km south of the Saskatchewan River. Then, when winds changed to easterly for a few days, some of these same black flies were redirected toward Saskatoon and beyond, apparently travelling a total distance of more than 300 km.

S. luggeri also regularly infiltrated forested areas against prevailing winds. Pastures along the northern edge of the Nisbet Forest reserve near Choiceland and Smeaton were chronically affected by dense swarms of *S. luggeri* regardless of wind directions. Every summer swarms moved through trees, often against prevailing winds, at least 30 km from breeding sites in the Saskatchewan River.

3. *S. luggeri* adults caused hyperactivity, panic and stampeding in livestock by swarming densely around the animals' heads. Animals ceased grazing and breeding when under severe attack. Calves could not nurse properly when herds were tightly packed and in constant turmoil and with peripheral animals forcing themselves into the herds. Calves also suffered malnutrition when milk flow from cows was reduced. Also, since *S. luggeri* adults bit animals around their eyes and udders, they may well have been instrumental in carrying disease organisms responsible for bovine keratitis and mastitis. Increased incidences of these diseases as well as stress-related diseases such as hoof rot in mature animals, and pneumonia and scours in calves always accompanied severe outbreaks of *S. luggeri*. In comparison, *S. arcticum* adults did not swarm intensively around animals' heads but concentrated their attacks along underlines, often unnoticed by victims. No animals died suddenly after being bitten by *S. luggeri* as had happened frequently with *S. arcticum* (Fredeen, 1981). However, during outbreaks of *S. luggeri* some animals died during stampedes, suffered broken limbs and had to be destroyed, or died from stress-related diseases. Pastures were unevenly grazed when cattle refused to stay in rich lowlands. Supplementary feeding was required, especially for bulls, as well as additional veterinary and labour services.

4. Unlike those of *S. arcticum*, adults of *S. luggeri* actively attacked people as well as other warm-blooded animals, except birds.

5. A major cause for ineffectiveness of larviciding against *S. luggeri* became apparent in later years when tests showed that a single injection of methoxychlor into the shallow, weedy Saskatchewan River often was not effective beyond 20 to 30 km downstream. In comparison, a single injection into the North Saskatchewan River in 1973 (fairly weed-free at that time) had been reasonably effective against *S. arcticum* larvae throughout at least 160 km (Fredeen, 1975).

6. An unexpected effect of larvicide treatments was that certain larvae removed from the Saskatchewan River (south branch in particular) apparently drifted downstream to reattach in suitable sites, often in the main Saskatchewan River downstream from the confluence of the south and north branches (Fredeen, 1983). Major outbreaks in 1977, 1978 and 1982 (not discussed in this paper) were believed to have resulted, at least in part, from downstream accumulations of reattached larvae following larvicide treatments further upstream.

For these reasons, sporadic outbreaks of *S. luggeri* continued to plague portions of east-central Saskatchewan in 1976 through 1982 during development of abatement strategies and studies of environmental effects of larvicide injections into the Saskatchewan River.

COMPLAINTS FROM RESIDENTS IN REGIONS AFFECTED BY OUTBREAKS IN 1978

Outbreaks of *S. luggeri* in 1978 were more widespread and damaging than in any year since outbreaks commenced in 1972. In 1978 I received more than 100 written complaints and petitions from at least 46 mailing centers, and many telephone calls from these and other districts. Most complaints of sustained severe attacks came from within about 100 km of the river, but others came from up to or even beyond 200 km (Fig. 4). In many districts there were few remissions from outbreaks from June through August.

A selection of quotations from people personally attacked in 1978 included: "dense swarms of black flies attacked like angry bees all day; many people wore netting when working outside, others carried portable smudges; repellents did not provide sufficient protection; fence and machinery repairing, construction work, telephone line repairs and other outside jobs were at times impossible, even with use of repellents; repellents did not prevent densely-swarming black flies from entering nose, mouth, eyes and ears; some people required medical attention for bites; rural and urban people alike lost many days of out-of-doors work and recreation, children and older people were unable to work or play out-of-doors; farm work was neglected when cattle required so much additional attention; air cleaners on tractors required daily servicing to remove black flies."

Remarks from people concerned about welfare of livestock in 1978 (owners, veterinarians and government employees) included: "milk production greatly reduced when animals unable to graze; increased incidence of mastitis believed caused by black flies which sometimes caused udders to drip with blood; cows with irritated udders produced less milk and could not tolerate nursing calves; cattle were in constant motion and stampeded frequently because of black flies swarming densely around their heads; a stampeding herd tore down a fence; cattle refused to graze outside until after sunset and thus required supplementary food; cattle bunched on hilltops or near farmyards; where there was access to mud or manure beds, cattle stood or lay in them; cattle crowding into a shed pushed out rear wall; cattle became noticeably thinner in pastures instead of showing expected weight gains; cattle unable to breed; bulls became impotent because of black fly attacks; calves burnt when pushed by herds into smudges; cattle

broke shoulders and limbs during stampedes; cattle in feed lots sold prematurely to avoid further weight losses; greatly increased incidences of bovine keratitis, mastitis, foot rot, calfhood scours and pneumonia blamed on extraordinary physical and nutritional stresses imposed by severe black fly attacks; livestock owners found it difficult to approach or herd animals in pastures; extra riders hired to cope with hyperactive herds; horses difficult to manage when under attack; horses, cattle, sheep and hogs had to be fed indoors; dogs severely bitten; moose and elk submerged themselves in water and were oblivious to human presence."

COMPLAINTS FROM PATRONS AND MANAGEMENT OF ONE LARGE PASTURE

Following the severe outbreaks of 1978, Mr. Stephen Burkell, Director of Pastures for the Prairie Farm Rehabilitation Administration for northeastern Saskatchewan, and I were invited to attend an annual meeting of directors and management of the James Smith Pasture to discuss complaints. This pasture, with an area of 3,230 ha, is located north of Kinistino (Fig. 4) and has, as its northern boundary, the main Saskatchewan River from whence repeated outbreaks of *S. luggeri* had emerged in 1978 and in two previous years.

Eight hundred and forty cows, many accompanied by suckling calves had been received into this pasture during the last week of May in 1978 and discharged 140 days later in mid-October. Patrons had expected cows and suckling calves to gain significantly in weight and had expected timely conceptions of cows from use of 35 high quality, purebred bulls. Management had expected minimal handling problems and uniform grazing of grasslands. Due to severe and prolonged outbreaks of *S. luggeri* these expectations were not realized.

Approximately 260 ha of lowlands in this pasture, including some of the richest grasslands, were not grazed in 1978. Although cattle were herded into those lowlands several times that summer, they would not stay because of continuous presence of black flies. Instead, cattle often congregated on overgrazed hilltops, apparently to take advantage of winds.

Management reported that five purebred bulls out of the 35 in service that summer had to be replaced when they became impotent due to severe debilitation and infections of the sheath and scrotum from black fly bites. Replacement costs totalled \$11,250.00 among bulls alone, despite daily supplemental feeding and adequate veterinarian services (Table 2).

Of 840 breeding cows in that pasture in 1978, there were only two fatalities attributed directly to black fly attacks (Table 2). Both animals suffered broken limbs during stampedes and had to be destroyed. Prompt attention saved many other sick animals, especially those with bovine keratitis (pinkeye), mastitis and foot rot.

Another loss, more difficult to assess, was an increase in proportions of cows showing delayed conceptions (Table 2). Our observations during outbreaks in 1978 confirmed producers' complaints that breeding was completely interrupted whenever animals came under severe attack. Mr. Allan Blair, Livestock Specialist for Saskatchewan Agriculture in east-central Saskatchewan, estimated that more than 20 percent of all cows in outbreak areas conceived at least one month later than expected in 1978. A calf born one month late the following year would have been about 30 kg lighter than expected at weaned-calf sales in the fall. The average price for weaned calves in Saskatchewan in the fall of 1979 was \$2.20/kg, indicating losses of \$66.00 for each weaned calf born one month later than expected. Thus if 20 percent of the cows in this pasture were affected in 1978, the resultant 168 conceptions, late by only one month each would have caused a loss of more than \$11,000.00 in the following year (Table 2). Losses from conceptions delayed for more than one month were not estimated. Allan

Blair estimated that the number of cows not conceiving at all in 1978 increased by at least two percent over that observed in 1977. However, conception rates also vary between herds according to culling and other management practices.

Ryan and Hilchie (1980) reported that, in areas of central Alberta affected by severe outbreaks of *S. arcticum* from the Athabasca River in 1978, 44 percent of calves born the following year were later than expected. In areas less affected by outbreaks, 21 percent of all calves were born later than expected. They also reported that non-conception rates varied from 8.41 to 12.17 percent in severely affected regions, but only 1.26 to 6.35 percent in areas less affected.

The major loss among beef cows in the James Smith pasture undoubtedly consisted of unrealized weight gains. Livestock owners and pasture managers unanimously claimed that their animals had lost weight during the 140-day grazing season in 1978 whereas past experience had led them to expect gains of about one kg per day. Photographs taken of herds in that pasture indicated that animals actually appeared thin when compared with unaffected animals from pastures further south. However, animals were not weighed in or out of the James Smith pasture and thus owners' claims could not be verified. To estimate values of unrealized weight gains I have used data obtained in 1982 from two herds of purebred hereford cattle pastured near Choiceland, Saskatchewan. In one of those herds, partly protected from attacks by *S. luggeri* with use of fenvalerate-impregnated ear tags (Bovaid[®], cows with suckling calves showed average individual weight gains of 0.967 ± 0.342 kg per day, whereas cows from an adjacent "unprotected" herd showed average gains of only 0.508 ± 0.270 kg per day, a difference of about 0.46 kg per day. Bovaid[®]-"protected" dry yearlings without calves showed an average advantage of about 0.57 kg per day over "unprotected" dry yearlings. Thus for the James Smith herd, of 838 surviving cows I have assigned weight gains of 0.5 kg per day per cow in 1978 instead of 1.0 kg that might have been realized had there been no black flies. Even this partial loss would have cost producers \$102,655.00 (Table 2).

There were 700 suckling calves in the James Smith pasture in 1978 and deaths of 12, valued at \$4,230.00, could be attributed directly to black fly attacks. Some of these calves had suffered fatal trampling injuries; others had died from nutritional and physical stress-related diseases such as scours and pneumonia. But again, main losses were unrealized weight gains due in part to delayed conceptions the previous year as discussed above and in part to hyperactivity and inability to suckle or graze properly in 1978. Milk production from beef cows in 1978 would have suffered long-term reductions similar to those for dairy cows, discussed later. Owners claimed that the average weight of a weaned calf from this pasture at fall sales of weaned calves was about 135 kg as compared to about 180 kg for weaned calves from pastures further south and less affected by black flies. This indicated that unrealized weight gains for suckling calves in the James Smith pasture averaged 0.32 kg per day per calf. Producers did not provide proof of these claims. Thus I have calculated losses on the basis of data obtained from test herds near Choiceland in 1982 and Prince Albert in 1979. At Choiceland, suckling calves from a herd partly protected from black flies for 100 days with the use of Bovaid[®] ear tags, gained an average of 0.121 kg more per day than similar calves in a nearby "unprotected" herd. Similar tests with Aberdeen Angus near Prince Albert in 1979 showed that calves from a herd protected for about 18 days with permethrin spray gained, on the average, 0.092 kg more per day than calves from a nearby "unprotected" herd.

Thus, while there were no reasons to doubt producers' claims of unrealized weight gains of 0.32 kg per calf per day for animals severely affected in the James Smith pasture in 1978, I

have assigned losses of 0.1 kg per calf per day. This would have amounted to an average loss for the 140-day grazing season of \$28.00 per calf for a herd total of \$19,260.00 (Table 2). This would have been additional to losses caused by delayed conceptions calculated earlier.

While compensatory weight gains could have occurred after black fly outbreaks ceased in the fall, losses calculated from unrealized weight gains described above for pastured cattle should be considered real losses for producers. Many animals, especially suckling calves and yearlings, were sold in the fall soon after leaving summer pastures, before compensatory gains could occur. Other animals, overwintered on home farms, could have achieved compensatory gains only at the expense of forages grown in home pastures or of forages especially harvested for use in winter.

Thus, total losses, conservatively estimated for the 140-day grazing season in 1978, in this one community pasture, apparently exceeded \$150,000.00 (Table 2). Costs not included in these calculations were veterinarians' fees and medications required to treat 260 cases of bovine keratitis, mastitis, foot rot, scours and pneumonia in excess of those treated the previous year, as well as costs of supplementary feeding, fence repairs, daily smudge building, increased animal insurance costs and hirings of extra riders to handle hyperactive herds and to monitor herds for sick animals.

ESTIMATED FINANCIAL LOSSES TO BEEF PRODUCERS IN AREAS OF EAST-CENTRAL SASKATCHEWAN AFFECTED BY SEVERE OUTBREAKS OF *S.* *LUGGERI* IN 1978

Regions where repeated complaints of damage to livestock originated during outbreaks in 1978 (Fig. 4) included about 5,700 km² (approximately 0.5 percent of Saskatchewan's Crop District 6, 13.0 percent of District 8 and 1.5 percent of District 9). Cattle populations in those portions of the three districts included at least 650 bulls, 11,000 beef cows, 9,500 suckling calves, 1,100 dairy cattle and 7,000 other cattle (mainly 1- to 2-year old steers, heifers and bulls). Practically all would have been either purebred or high-quality crossbred animals. Some bulls and other cattle would have had access to indoor feeding during outbreaks.

In September, 1978, 39 livestock owners in six municipalities (Numbers 399, 400, 429, 430, 459 and 460, Fig. 6) were asked by the local Agricultural Representative, Eugene Bendig, to complete a form indicating effects of black fly outbreaks on their farms that year. Eleven reported that animals had to be housed much of the summer, three reported premature sales of animals including some animals blinded by bovine keratitis believed transmitted by infected black flies, and 10 reported fatalities caused by black flies of 14 calves, nine yearlings, three cows and three bulls. All claimed that pastured animals became thinner during the summer and also that outbreaks caused prolonged and severe disruptions of all outdoor activities.

George O'Bertos, Director, Saskatchewan Lands Branch, Tisdale, reported that in every provincial community in his jurisdiction, 12 to 20 calves in each population of 800 to 1,000 calves per pasture were killed by black flies that summer. These calf fatalities of 1.5 to 2.0 percent were comparable to the loss of 1.72 percent reported that same year for the James Smith pasture.

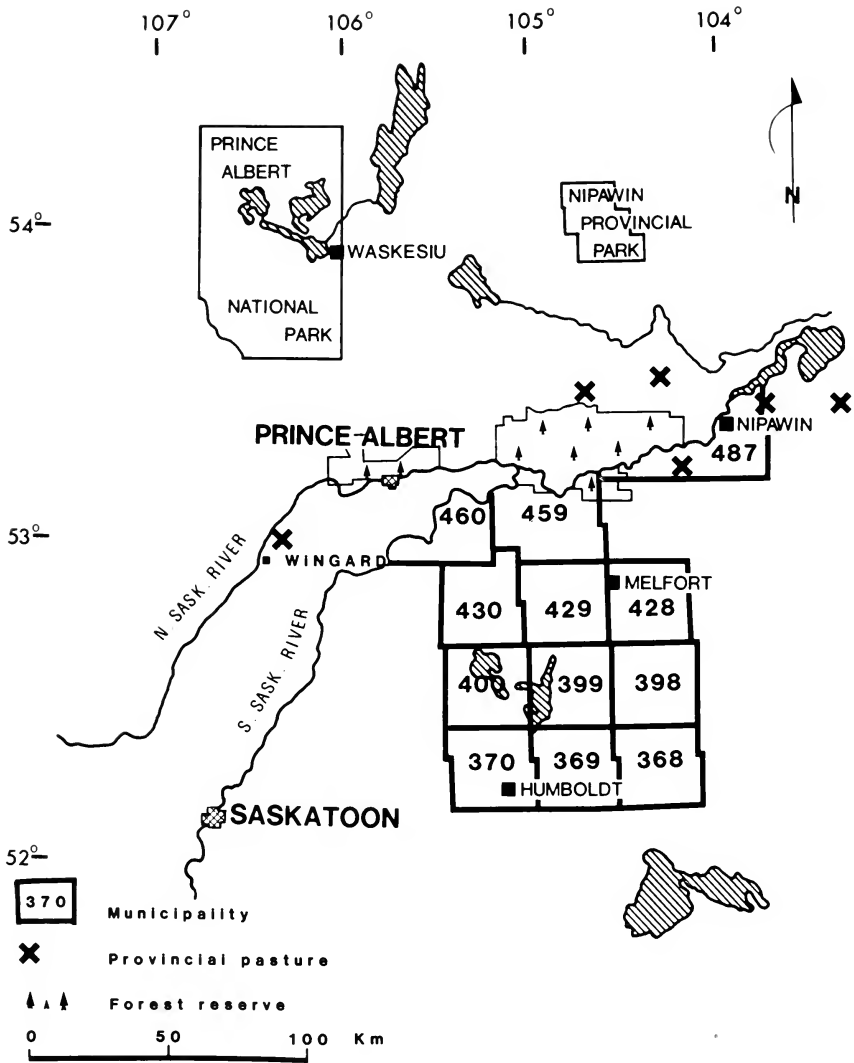


Fig. 6. Map of central Saskatchewan showing locations of 6 provincial community pastures in which cattle were reported to have been affected by black flies in recent years, and 12 municipalities affected by different intensities of outbreaks of *Simulium luggeri* in 1976 through 1981.

TABLE 2. ESTIMATED VALUES OF BEEF CATTLE LOSSES IN THE JAMES SMITH COMMUNITY PASTURE NORTH OF KINISTINO, SASKATCHEWAN DUE TO REPEATED OUTBREAKS OF BLACK FLIES, *SIMULIUM LUGGERI* IN 1978.

Category	Number of	Type of loss	Animals affected		Net loss per	
	animals in		(no.)	(%)	affected	Total value
	pasture				animal (\$)	of losses (\$)
Bulls	35	Fatalities	0	0.00	—	—
		Replacements	5	14.30	2,250.00 ⁽¹⁾	11,250.00
Cows	840	Fatalities	2	0.24	787.50 ⁽²⁾	1,575.00
		Delayed				
		conceptions	168	20.00	66.00 ⁽³⁾	11,088.00
		Unrealized				
		weight gains	838	99.76	122.50 ⁽⁴⁾	102,655.00
Calves	700	Fatalities	12	1.72	360.00 ⁽⁵⁾	4,320.00
		Unrealized				
		weight gains	688	98.28	28.00 ⁽⁶⁾	19,260.00
TOTAL						
LOSSES						150,148.00

⁽¹⁾Replacement cost (\$3,000.00) minus commercial sale value (\$750.00).

⁽²⁾Estimated 450/kg animal at \$1.75/kg.

⁽³⁾Conception estimated to be at least 1 month late, with the weaned calf weight about 30 kg lighter than expected the following year with an average value of \$2.20/kg.

⁽⁴⁾Estimated 70 kg unrealized weight gain/cow at the end of the 140-day grazing season, with an average value of \$1.75/kg.

⁽⁵⁾Estimated 180 kg/weaned calf at \$2.00/kg in the fall of 1978.

⁽⁶⁾Estimated 14 kg unrealized weight gain/calf at the end of the 140-day suckling season at \$2.00/kg.

These data suggest that effects of outbreaks in 1978 on livestock outside the James Smith pasture were similar to those within. On that basis the following losses were calculated: If one-seventh of the 650 bulls died or required replacement at an average net loss of \$2,250 per bull, losses from this source would have totalled \$209,000. An estimated 26 beef cows and 160 suckling calves, valued at more than \$78,000, may have been killed. If 20 percent of the 11,000 beef cows suffered delayed conceptions equivalent to single oestrus cycles with an average net loss of \$66 per calf at weaned calf sales the following year, losses from this source alone would have totalled \$145,200. But the largest financial losses would have resulted from unrealized weight gains for 11,000 beef cows, 9,500 suckling calves and 7,000 weaned cattle. Despite claims by most producers that their animals had actually lost weight during the summer-long outbreaks in 1978, I estimated from our tests reported earlier that suckling calves may have gained an average 0.1 kg per day (14 kg for the grazing season) and cows and weaned cattle 0.5 kg per day (70 kg for the season) instead of anticipated seasonal gains of 28 kg and 140 kg under black fly-free conditions. On this basis, unrealized weight gains for some 9,500 calves in severely affected areas in 1978 may have cost producers at least \$266,000 and for some 18,000 cows and immature cattle, \$2,205,000. Accumulated losses for all classes of beef cattle in severely affected areas thus were estimated to have exceeded \$2,903,000. These losses were calculated for only those areas totalling about 5,700 km² considered to be severely affected by black fly outbreaks in 1978. Losses in an additional 32,000 km² less severely affected (Fig. 4) were not included in these calculations. Also excluded were estimates of costs of supplementary feeding, especially for cattle kept indoors, supplementary feeding, especially for cattle kept indoors, supplementary labour, veterinary services, repairs to fences and barns, and increased insurance against future losses. Thus, actual losses to the entire beef cattle industry in east-central Saskatchewan in 1978 were believed to have been much larger than the \$2,903,000 shown in these calculations.

TRENDS IN CATTLE POPULATIONS IN PROVINCIAL COMMUNITY PASTURES AFFECTED BY BLACK FLY OUTBREAKS

Livestock producers anticipate advantages in committing cattle to community pastures. These pastures offer expansion of production beyond home pasture capacities as well as opportunities for quality grazing and quality breeding from registered herd sires or artificial insemination (A.I.). However, in large pastures animals cannot be given the same kind of individual attention available in small home pastures. Producers claimed that during black fly outbreaks their animals were subjected to severely debilitating stresses causing weight losses, sickness and missed oestrus cycles whether in natural or A.I. breeding programs. Because of this some producers ceased committing cattle to large pastures in regions prone to outbreaks of *S. arcticum* until 1973 and of *S. luggeri* after 1975. However, their places in pasture quotas generally were filled by other producers hopeful of improvements in black fly control measures.

There are three types of community pasture organizations in Saskatchewan: provincial, federal and co-operative. To investigate complaints from producers and pasture managers, numbers of cattle committed annually to six provincial community pastures in municipalities frequently affected by black flies (those bordering the Saskatchewan River between Wingard and Nipawin) (Fig. 6) were compared with numbers in all other 48 provincial community pastures in the province, 1969 to 1981, inclusive (Saskatchewan Agriculture, 1970-1982).

On average, less than 85 percent of official carrying capacities of "affected pastures" was used 1969 to 1981, inclusive, as compared with more than 89 percent for pastures in the remainder of the province (Fig. 7A). The difference was significant ($P = 0.05$). Pasture managers reported that some of the richest lowland areas often were undergrazed because cattle congregated on windy hilltops to avoid black fly attacks. Reduced usage of "affected" pastures was particularly noticeable before 1973 and after 1977.

Percentages of breeding cows among populations of mature cattle committed to "affected" pastures each year were consistently lower (some by as much as 14 percentage points) than populations in pastures in the remainder of the province ($P = 0.01$) (Fig. 7B). This supports claims by some owners that they withheld breeding cows with expectations of obtaining improved conception rates in home pastures.

Percentages of suckling calves among breeding cows committed to "affected" pastures were lower than in other provincial pastures in nine of the 13 years (Fig. 7C) but means for the 13 consecutive years did not differ significantly. In particular, conception rates appear to have been reduced during black fly outbreaks 1969 to 1973 (*S. arcticum*?) and 1976 to 1981 (*S. luggeri*) as claimed by livestock owners. In 1979, 6.5 percent fewer cows were accompanied by calves in "affected" pastures than in other provincial pastures, suggesting that average conception rates had been reduced by that amount during the severe outbreaks of 1978.

TRENDS IN CATTLE POPULATIONS AND LAND-USE PATTERNS IN DISTRICTS SUBJECTED TO CHRONIC OUTBREAKS OF *S. LUGGERI*, 1976 THROUGH 1981

Many livestock producers in outbreak areas stated that they reduced or even eliminated herds because black flies rendered their operations less profitable than expected. While numbers of dairy and beef cattle did decline in the entire province, 1975 to 1981, presumably for economic reasons, reductions were greatest in Crop District 8 (Figs. 1, 8) (Saskatchewan Agriculture, 1976, 1982). During those seven years, numbers of beef cattle declined by 27 percent in Crop District 8, 19 percent in District 9, and 21 percent in the remainder of the province. Numbers of dairy cattle declined by 32, 20 and 6.5 percent in those same three districts.

On a finer scale, largest declines occurred in municipalities bordering the Saskatchewan River (Fig. 6, Table 3). In three such municipalities where average distance from farm to river was about 13 km, dairy cattle numbers declined by 70.3 percent between 1971 and 1981 (Statistics Canada, 1973, 1983). Numbers of "other" cattle declined by 29.2 percent. At an average distance of 43 km, numbers declined by 52.5 and 15.1 percent, at 74 km by 47.3 and 1.7 percent, and at 101 km by 54.0 and 11.7 percent for dairy and "other" cattle, respectively.

Amounts of land devoted to improved pasture declined by 32.4 percent between 1971 and 1981 in municipalities averaging 13 km from the river, by 46 percent at 43 km and by 6.9 percent at 74 km, but increased by 10.4 percent at 101 km (Table 3). Amounts of land devoted to cultivated crops did not change in inverse proportions as expected. However, much of the land adjacent to the valley of the Saskatchewan River is classified as unsuitable for cultivation on account of steep contours, stoniness, light soil textures subject to wind erosion, and even high water tables. Thus it appears that some land withdrawn from use as cultivated pastures may have been abandoned when it became uneconomical to produce livestock. For instance, on farms averaging 13 km from the river in the three municipalities studied, 1,237 ha of land formerly classified as pastures, were unaccounted for in the Canadian Census of 1981,

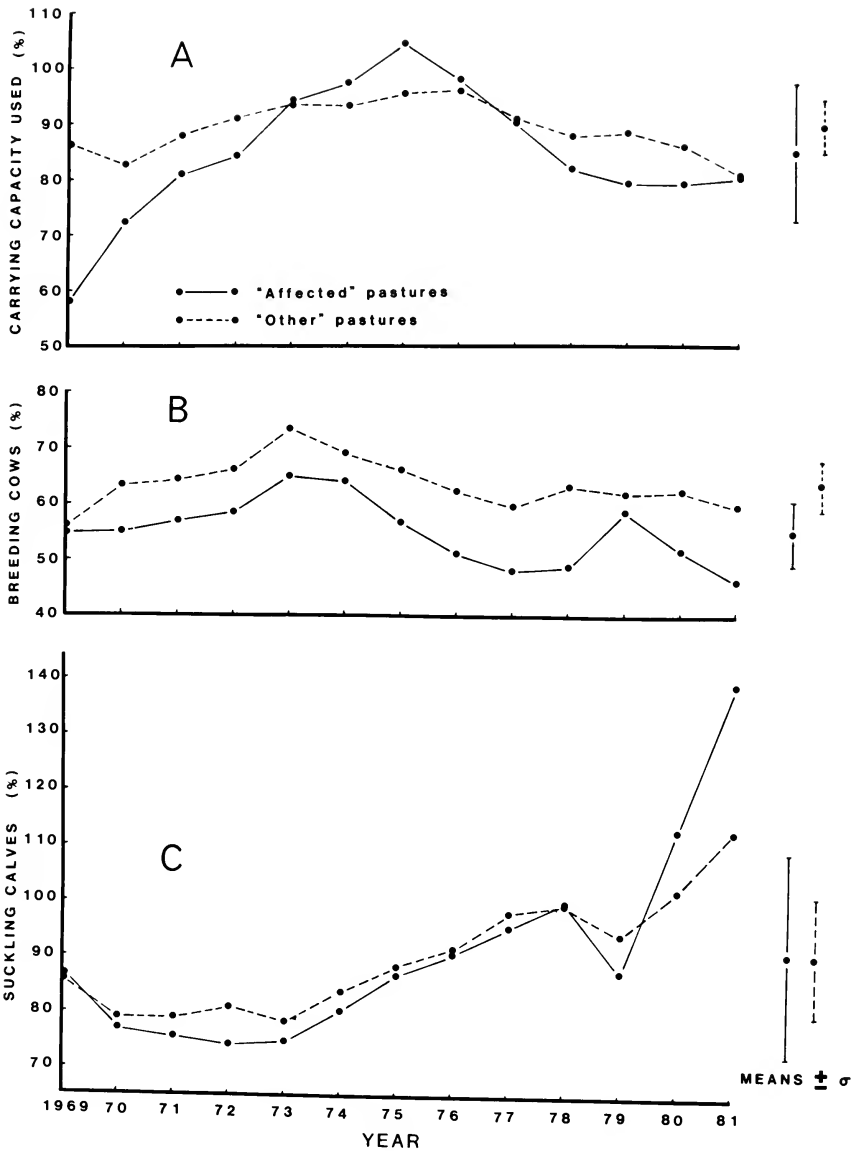


Fig. 7. Trends in populations of mature cattle, breeding cows and suckling calves, 1969 through 1981, committed to six provincial community pastures (see Fig. 6 for locations), in municipalities adjacent to the Saskatchewan River between Wingard and Nipawin in Saskatchewan (a region affected by chronic outbreaks of black flies), compared with numbers committed to community pastures in the remainder of the province: A - populations of mature cattle expressed as percentages of carrying capacities of those pastures; B - populations of breeding cows - expressed as percentages of total adult cattle assigned to those pastures; C - populations of suckling calves expressed as percentages of total breeding cows assigned.

TABLE 3. TRENDS IN CATTLE POPULATIONS, AND IN LAND AREAS DEVOTED TO IMPROVED PASTURES AND TO CULTIVATED CROPS, BETWEEN 1971 AND 1981, IN FOUR SETS OF MUNICIPALITIES LOCATED AT DIFFERENT DISTANCES FROM THE SASKATCHEWAN RIVER

Municipalities ⁽¹⁾	Trends, 1971 to 1981 (%) ⁽²⁾				
	Average	Cattle		Improved	Cultivated
	from river (km)	(excluding dairy cows)	Dairy cows	pasture	crops
368, 369, 370	101	-11.7	-54.0	+10.4	+ 6.3
398, 399, 400	74	- 1.7	-47.3	- 6.9	+ 2.3
428, 429, 430	43	-15.1	-52.5	-46.0	+ 7.1
459, 460, 487	13	-29.2	-70.3	-32.4	+ 0.1

⁽¹⁾See Figure 6 for locations of municipalities in relation to the Saskatchewan River.

⁽²⁾Calculated from census data (Statistics Canada, 1973, 1983).

suggesting abandonment.

LOSSES SUSTAINED BY MILK PRODUCERS DURING OUTBREAKS OF *S. LUGGERI*

Many dairy herds in central Saskatchewan are either kept indoors or at least allowed free access to barns. By 1982, in those areas around Prince Albert chronically affected by black fly outbreaks, only five of 18 producers still pastured their milking cows outside all summer. A number of other dairies ceased operations in recent years because they were unwilling to convert, in the face of chronic black fly outbreaks, to housing that would have been both capital and labour intensive.

Data about milk-shipments were obtained from three dairies for five consecutive years, 1977 to 1981, to determine whether outbreaks of *S. luggeri* affected productivity. None of 15 other dairies visited near Prince Albert were able to provide uninterrupted data for this 5-year period or even for the one year especially investigated, 1978. Dairies "A" and "B" (Fig. 4, 1978) were located in a region subjected to relatively severe outbreaks of *S. luggeri* at least during the first three summers of this study. Outbreaks at "c" were less severe. I did not obtain data from regions completely free of black fly outbreaks.

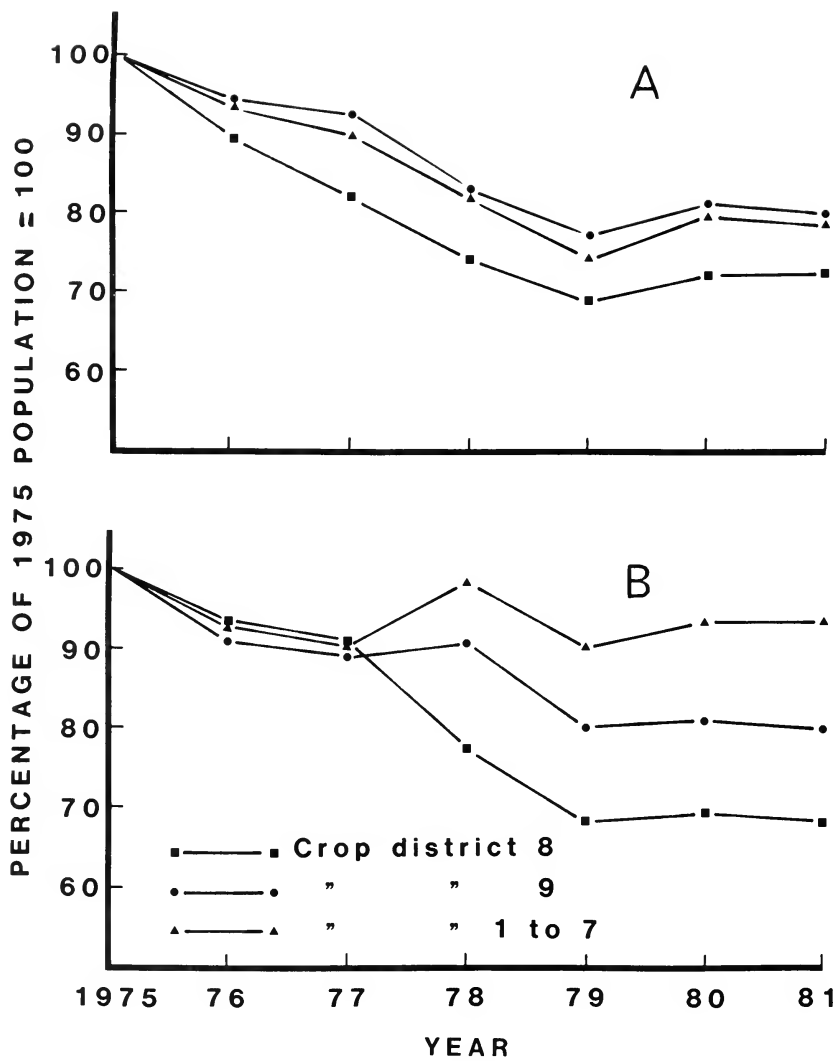


Fig. 8. Annual trends in populations of cattle on Saskatchewan farms expressed as percentages of 1975 populations in Crop Districts 8 and 9 (see Fig. 1 for locations) near the Saskatchewan River, and in the remainder of Saskatchewan: A - beef cows; B - milking dairy cows.

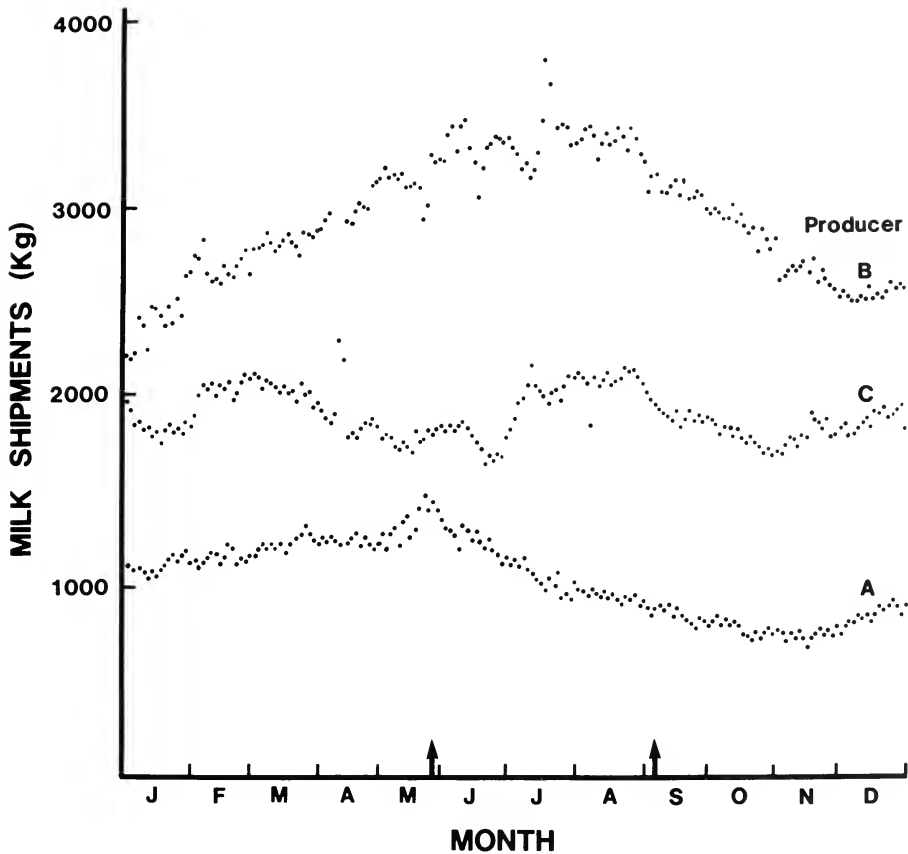


Fig. 9. Milk shipments (2-day accumulations) throughout 1978 from three dairies in areas of central Saskatchewan affected by chronic outbreaks of black flies (*Simulium luggeri*) (see Fig. 4, 1978, for locations of dairies). Arrows indicate commencement of outbreaks on May 26 and approximate ending 74 days later on September 7, 1978.

Producer "A" always pastured his milking cows outside all summer because of an abundance of rough, wet pasture lands that could not be used for grain or hay crops. He always provided supplementary cut fodder, outside, as required, in addition to the usual grain concentrates at milking time.

Milking cows of producer "B", located five to six km southeast of "A" were confined to the barn at all times. Producer "C" was located about 75 km southwest of "A" and "B", and although his cattle spent much time out-of-doors, they were allowed free access indoors at all times. He reported that his animals voluntarily remained indoors during fly outbreaks and were fed there.

These dairymen attempted to maintain uniformly high production to fulfill official milk quotas by providing high quality rations and by having cows freshen at uniform intervals. They reported that milk production increased significantly after cattle commenced grazing new grass

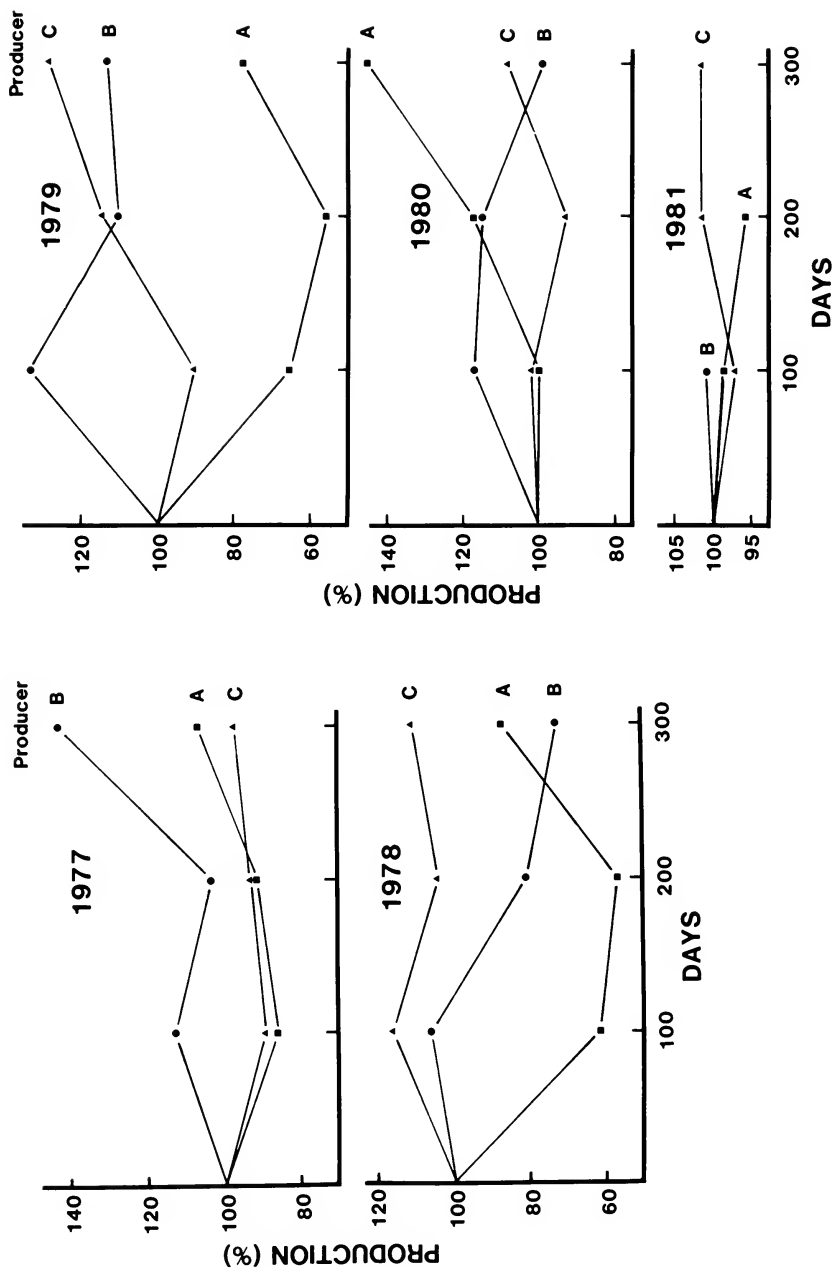


Fig. 10. Trends in volumes of milk shipments from three dairies in central Saskatchewan (see Fig. 4 for locations) in each of 5 years, 1977 through 1981. The "100-percent" starting point each year indicates average daily production throughout 10 days immediately before the beginning of outbreaks. Successive points thereafter at intervals of 100, 200 and 300 days after commencement of outbreaks represent percentages of that "pre-outbreak" production each year, also calculated from 10-day means.

TABLE 4. MILK PRODUCTION FROM THREE DAIRIES IN CENTRAL SASKATCHEWAN BEFORE AND AFTER COMMENCEMENT OF BLACK FLY OUTBREAKS (*S. LUGGERI* N. AND M.) ON MAY 26, 1978.

Average daily production during two 175-day periods, one immediately before and one immediately after commencement of outbreaks			Value of difference per cow per day**
Producer*	Before (kg)	After (kg)	Difference (kg) (\$)
A	585	480	-105 -0.95
B	1395	1605	+210 +0.71
C	954	974	+20 +0.11

*See Fig. 4 for locations of these dairies.

**Average number of lactating cows for producer A = 30, B = 80, C = 50. These producers received \$0.27 gross per kg of milk.

in the spring, but that it declined when black fly outbreaks commenced a few weeks later unless animals were protected. Producer "A" reported that production did not return to expected levels during lulls in outbreaks but only after affected animals commenced new lactation cycles, in many instances long after outbreaks had ceased in the fall. This was particularly noticeable when stress had been severe and long-lasting, as in 1978. Milk shipment data provided by "A" indeed showed both immediate and long-term effects (Fig. 9). In 1978 outbreaks commenced on May 26 and a decline of 3.0 percent in milk production was already evident in the 2-day accumulation shipped on May 27. By the time outbreaks ended in early September production had declined by about 40 percent from what it had been during the week before outbreaks commenced on May 26. This decline did not end until mid-November, about 175 days after outbreaks had commenced. In contrast, production from herds "B" and "C" increased during this same 175-day outbreak period (Table 4). Similar long-term effects from outbreaks of *S. luggeri* were noted in 1979, but not in 1977, 1980 or 1981 (Fig. 10) when outbreaks of black flies south of Prince Albert were relatively light.

In 1978 producers received \$0.27 per kg of raw milk. Throughout the first 175 days after outbreaks commenced on May 26, the decline in production in herd "A" resulted in an average reduction in gross returns of \$0.95 per cow per day when compared with average production in that same herd throughout 175 days immediately preceding May 26 (Table 4). In contrast, production increased in herds "B" and "C" between these same two 175-day periods, resulting in average increases in gross returns of \$0.71 and \$0.11 per cow per day. Production trends in herds "A" and "C" may be compared because both herds were pastured during the summer of

1978. Management in those two herds differed mainly in that herd "A" grazed out-of-doors all the time but herd "C" had free access to a barn especially during outbreaks and were fed indoors as required. The difference in average gross returns between these two herds for the two consecutive 175-day periods was \$1.06 per cow per day for a total of \$185.50 per cow. Total confinement indoors as in herd "B" resulted in an even larger improvement in gross returns.

In those portions of Crop Districts 8 and 9 totalling some 5,700 km² that were most severely affected by black flies in 1978, there were estimated to have been about 310 lactating dairy cows (including herd "A"), which did not have free access to barns during outbreaks. Assuming that those animals were affected similarly to those in herd "A", lost production would have exceeded \$57,500 during the first 175 days after outbreaks commenced. Additional to this would have been costs of supplementary feeding, veterinary services, extra manpower required to handle hyperactive herds, as well as general milk volume reductions in an additional 32,000 km² of farm lands that were less severely affected by black flies. Producers also claimed that there were some delayed conceptions as noted for beef cattle. Thus total losses to the dairy industry in Saskatchewan due to outbreaks of *S. luggeri* in 1978 must have greatly exceeded \$57,500.

DISCUSSION AND CONCLUSIONS

The purpose of this paper was to catalogue losses attributed to outbreaks of the black fly *S. luggeri* in Saskatchewan, and to attempt to evaluate losses to determine whether demands for abatement programs by livestock producers and other residents of east-central Saskatchewan were justified.

Residents in this part of Saskatchewan have had to contend with black fly problems since the earliest days of settlement because the Saskatchewan River has always provided breeding sites for large numbers of larvae. Until about 1976, outbreaks of *S. arcticum* could be expected every year. Larvae of *S. luggeri* replaced those of *S. arcticum* when the river became shallow, clear and weedy every summer, mainly due to upstream storage of water in new hydropower reservoirs. Annual outbreaks of *S. luggeri* commenced on a large scale in 1976 and have continued to the present time although moderated on many occasions by experimental injections of methoxychlor larvicide into the Saskatchewan River.

Animals did not die suddenly after attacks by *S. luggeri* as had happened with *S. arcticum*. Nevertheless, outbreaks of *S. luggeri* inflicted significant losses for several reasons. Losses were enhanced, in part, by emergence of enormous numbers of adults from larvae breeding in vast new weed beds in the Saskatchewan River. Also because *S. luggeri* is multivoltine, in the absence of larviciding, numbers increase during summer months. In 1978 during the worst outbreaks on record, black flies emerged from the river throughout late May to late September and spread into at least 38,000 km² of surrounding countryside. About one-seventh of this area was subjected repeatedly to severely damaging outbreaks that year. Searches for larvae in other nearby breeding sites such as the Carrot and Torch Rivers showed that only the Saskatchewan River was capable of producing outbreaks of such magnitude. *S. luggeri* swarmed aggressively around heads of animals on most warm days that summer forcing animals into almost continuous hyperactivity. Animals stampeded readily, spent much time on windy hilltops and greatly reduced breeding activities. People were unable to perform normal outdoor activities because they too were attacked. Producers, who generally had been satisfied with the abatement program developed to prevent outbreaks of *S. arcticum*, demanded similar

protection from outbreaks of *S. luggeri*. But whereas single larvicide injections, sometimes confined to a single branch of the Saskatchewan River, generally were sufficient to prevent outbreaks of *S. arcticum*, multiple injections both as regards times and sites often were required for *S. luggeri* partly because it was multivoltine and partly because single injections were no longer effective beyond 20 to 50 km in these weedy rivers. Such an intensive larviciding program would not be considered acceptable on a continuous basis without adequate economic justification, not only because of cost of larvicide but also because of concerns for non-target organisms in the river. Larvicide for a single, annual program as intensive as that required in 1979 (Fredeen, 1983) could cost as much as \$25,000 at 1983 prices. Studies of environmental effects of using methoxychlor as a larvicide, including residue persistence and long-term effects on non-target invertebrates, indicated that environmental effects were negligible and might be tolerated in the event of proof of need for larviciding (Fredeen *et al.* 1975; Fredeen, 1983).

Studies of outbreaks of *S. luggeri*, from 1976 to the present time and especially of severely disruptive outbreaks in 1978 showed that losses to livestock owners could greatly exceed the cost of even the most expensive larviciding program envisaged. Losses from a single large pasture (James Smith Community Pasture) containing about 1,575 beef animals were estimated to have exceeded \$150,000 in 1978. Losses included costs of replacing purebred bulls which had become impotent due to severe debilitation, fatalities of cows and calves, unrealized weight gains and losses due to delayed conceptions. About 20 percent of the cows were said to have missed being bred for at least one oestrus cycle that summer and numbers of cows not bred at all increased by at least 2.0 percent from the previous year. Not included in the calculations were costs of supplementary feeding, fence repairs, wages for extra riders, increased insurance costs, veterinarians' fees and medications for about 260 cases of pinkeye, foot rot, scours and pneumonia additional to those seen the previous year.

The James Smith pasture represented less than 0.6 percent of the entire area that was severely affected by outbreaks in 1978 judging by telephone calls, letters and personal interviews with producers. In this 5,680 km² area there were many herds of beef cattle containing about 650 bulls, 11,000 cows, 7,000 weaned cattle and 9,500 suckling calves. Losses estimated on the same basis as those for the James Smith pasture exceeded \$2,900,000. Again, calculations did not include many miscellaneous costs, nor any losses in the remaining 32,000 km² of farmlands that were occasionally affected by outbreaks in 1978.

Dairy producers, who were unable to provide housing and indoor feeding for their milking animals, also suffered considerable losses. Average gross financial returns from two pastured herds in 1978, one having free access to a barn during outbreaks and one without access to shelter, differed by \$185.50 per animal for the first 175 days after outbreaks commenced on May 26, when compared with returns during 175 days immediately preceding outbreaks. Total losses for some 310 unprotected milking cows in 5,680 km² of severely affected farm lands in 1978 were estimated to have exceeded \$57,500. Calculations did not include production losses from the remaining 32,000 km² of farm lands affected by lighter outbreaks that year or costs of supplementary feeding, management or veterinarians' services.

Fear of chronic outbreaks caused many beef and dairy cattle producers to reduce or even eliminate herds in recent years. Data from provincial and federal government sources indicated that trends in animal populations and land-use patterns differed between regions affected by chronic black fly outbreaks and the rest of the province. For instance, between 1975 and 1981 in Crop District 8 (relatively most affected by outbreaks), numbers of beef cattle declined by 27 percent and dairy cattle by 32 percent. In the remainder of Saskatchewan, numbers declined

by 21 and 6.5 percent during these same six years. Pasture lands were either converted to less productive uses or abandoned.

Concerns about black fly outbreaks have not lessened since *S. luggeri* replaced *S. arcticum* in the Saskatchewan River in the early 1970's. Summer-long outbreaks of *S. luggeri* have on occasion caused enormous losses to livestock producers. In addition, people are attacked so vigorously that sometimes they are not able to work out-of-doors. Control measures against *S. luggeri* must be continued and it seems most logical to apply control while black flies are in the larval stages, confined to relatively limited breeding sites in the Saskatchewan River. Dispersions of adults are unpredictable and often widespread once they have left breeding sites. Alternative methods of providing protection for livestock and people are under investigation, but at present best protection is provided with larvicide used in accordance with permits renewed annually by federal and provincial authorities.

Experimental manipulation of water flow in the Saskatchewan River seems remote because approved uses already tax limited water resources. Ongoing tests with insecticides against adults of *S. luggeri* indicate that ear tags impregnated with synthetic pyrethroids may provide relief in large herds. Managers of the 3,230 ha James Smith Community Pasture, already convinced of their usefulness, have not accepted untagged animals in that pasture since the spring of 1981. Results from larvicide tests with *Bacillus thuringiensis* serotype H 14, conducted by the Canada Biting Fly Centre, Winnipeg, should be known by 1985.

It is hoped this paper will help provide a balanced view for decision makers, when used in conjunction with an earlier paper on environmental effects of use of methoxychlor larvicide (Fredeen, 1983). Environmental issues involved must be studied in the broadest sense with concerns balanced between potential effects of chemical larvicides upon non-target species inhabiting or otherwise using Saskatchewan River water, and potential effects of black fly outbreaks upon people in their terrestrial environment, if larvicide is used ineffectively or not at all.

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THE NEARCTIC SPECIES OF THE GENUS *PSEUDOMYRMEX* (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

The Nearctic ants of the genus Pseudomyrmex are revised, with the consequent recognition of ten species, belonging to three species groups: gracilis group (P. mexicanus Roger), elongatus group (P. cubaensis Forel, stat. nov.; P. elongatus Mayr), and pallidus group (P. apache Creighton; P. brunneus F. Smith; P. ejectus F. Smith; P. leptosus Ward, sp. nov. [type locality: Payne's Prairie, 8 mi. S. Gainesville, Florida]; P. pallidus F. Smith; P. seminole Ward, sp. nov. [type locality: John Pennekamp State Park, Munroe Co., Florida]; P. simplex F. Smith). P. peruvianus Wheeler, stat. nov., described as a variety of P. ejectus, is considered a distinct species. The following are proposed as new synonyms of P. simplex: P. delicatulus Forel = P. capperi Forel = P. panamensis Forel = P. vittatus Forel. The Nearctic Pseudomyrmex are characterized by marked geographical variation, coupled with the frequent occurrence of sympatric sibling species.

RÉSUMÉ

Les fourmis Néarctiques du genre Pseudomyrmex sont révisées, avec la reconnaissance résultante de dix espèces, appartenant de trois groupes d'espèces: groupe gracilis (P. mexicanus Roger), groupe elongatus (P. cubaensis Forel, stat. nov.; P. elongatus Mayr), et groupe pallidus (P. apache Creighton; P. brunneus F. Smith; P. ejectus F. Smith; P. leptosus Ward, sp. nov. [lieu d'origine du type: Payne's Prairie, 8 mi. S. Gainesville, Florida]; P. pallidus F. Smith; P. seminole Ward, sp. nov. [lieu d'origine du type: John Pennekamp State Park, Munroe Co., Florida]; P. simplex F. Smith). P. peruvianus Wheeler, stat. nov., décrite comme une variété de P. ejectus, est considéré une espèce distincte. Les noms suivant sont proposés comme nouveaux synonymes de P. simplex: P. delicatulus Forel = P. capperi Forel = P. panamensis Forel = P. vittatus Forel. Les Pseudomyrmex Nearctiques sont caractérisés par variation géographique marquée, accompagnés de l'occurrence fréquente des espèces sympatriques très similaires.

INTRODUCTION

The predominantly Neotropical ant genus, *Pseudomyrmex*, is fraught with species-level taxonomic problems. Among the few species which occur in the United States, those allied to *P. pallidus* have been repeatedly confused (e.g., Creighton, 1950). This is partly due to the failure of earlier taxonomists to examine relevant type material, exacerbated by the existence of sibling species and extensive geographical variation. Preparatory to a more comprehensive revision of the *pallidus* group in the Neotropical region, I here present a review of all *Pseudomyrmex* species in the United States, most of which belong to the *pallidus* group. This allows the methodological groundwork to be presented and permits clarification of the identity of several common species.

The North American *Pseudomyrmex* literature is summarized in D. R. Smith (1979). Creighton (1950) recognized four species, described one more in 1952, and gave a key to the

United States species in 1955. In the present treatment I recognize nine North American species, of which two are new. In addition I have included one other species which ranges up to the margin of the Nearctic region in northern Mexico. Since there has been widespread misidentification of Nearctic *Pseudomyrmex*, literature records for most species need to be reconfirmed. I have attempted to determine the identity of species cited in the North American literature, in those cases where associated museum material has been available for examination.

A salient feature of the *Pseudomyrmex pallidus* group (and perhaps a characteristic of the genus as a whole) is the frequent occurrence of two or more closely related species in a given locality. There are usually small but reliable morphological differences which serve to distinguish the members of such sympatric assemblages. However these locally diagnostic characters show a marked propensity towards geographical variation. Thus, establishing the diagnostic features of species (as opposed to local populations) requires the examination of specimens from a broad geographical area. In the present context, this has meant examining material from both North and Central America since most of the Nearctic species are not confined to the United States. Moreover, since the characters often involve aspects of size and shape, it has been necessary to make a rather large number of metric measurements in order to accurately assess the limits of intra- and interspecific variation. The keys to Nearctic species depend to some extent on these measurements.

Descriptions of the worker caste of each species have been kept concise, with descriptive details encapsulated in the ranges of 19 measurements and indices which precede the diagnosis (expanded to 26 metrics for new species). This helps to standardize and economize the descriptive process. It also deemphasizes the kind of typological thinking which is likely to impede taxonomic progress in *Pseudomyrmex*. In this regard, the illustrations should be used prudently; they represent "typical" specimens, but reference should also be made to the keys and species descriptions where the known bounds of variation are indicated.

MATERIALS AND METHODS

Collections are referred to by the following abbreviations:

- BMNH British Museum of Natural History, London
- GCW G. C. & J. Wheeler collection, San Antonio, TX
- LACM Los Angeles County Museum, Los Angeles, CA
- MCSN Museo Civico di Storia Naturale, Genoa, Italy
- MCZ Museum of Comparative Zoology, Cambridge, MA
- MHN Muséum d'Histoire Naturelle, Geneva, Switzerland
- MNHU Museum für Naturkunde der Humboldt-Universität, Berlin, D. D. R.
- NHMB Naturhistorisches Museum, Basel, Switzerland
- NHNV Naturhistorisches Museum, Vienna, Austria
- PSW P. S. Ward collection, University of California, Davis, CA
- UCD Bohart Museum of Entomology, University of California, Davis, CA
- USNM National Museum of Natural History, Washington, DC

Scanning electron micrographs were taken with a Philips SEM 501, using gold-palladium coated specimens. Precautions were taken to avoid distortion of the micrograph by (i) careful positioning of the specimen on the stub, and (ii) measuring the CRT image with calipers and making any tilt-correction necessary to restore the true proportions.

Terms for integument sculpture are taken from Harris' (1979) glossary.

Metric measurements were made at 50X power on a Wild microscope, with a Nikon micrometer wired to an Autometronics digital readout. All measurements were made in millimeters, to the nearest thousandth of a millimeter. Most have been rounded to two decimal places for presentation here.

The following measurements are cited (when the head is held in full-face, dorsal view, it is positioned so that the median ocellus and the frontal carinae lie in the same focal plane):

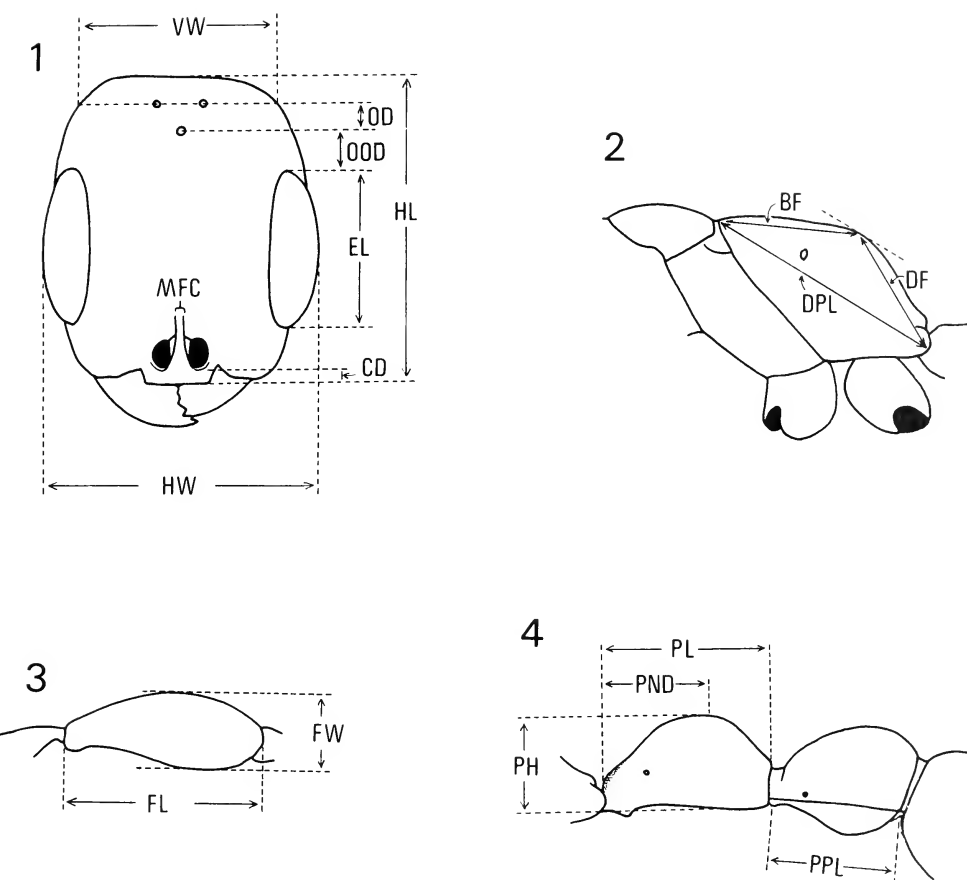
- HW Head width: maximum width of head, including the eyes, measured in full-face, dorsal view (Figure 1).
- VW Vertex width: width of the posterior portion of the head (vertex), measured along a line drawn through the lateral ocelli, with the head in full-face, dorsal view (Figure 1).
- HL Head length: midline length of head proper, measured in full-face, dorsal view, from the anterior clypeal margin to the midpoint of a line drawn across the occipital margin (Figure 1).
- EL Eye length: length of compound eye, measured with the head in full-face, dorsal view (Figure 1).
- OD Ocellar distance: distance from the middle of the median ocellus to the midpoint of a line drawn between the lateral ocelli. measured with the head in full-face, dorsal view (Figure 1).
- OOD Oculo-ocellar distance: distance from the middle of the median ocellus to a line drawn across the posterior margins of the compound eyes (Figure 1) (this distance is negative in value if the posterior margin of the compound eye exceeds the median ocellus).
- CD Clypeal distance: distance from the anterior clypeal margin to a line drawn across the anterior margins of the frontal carinae (Figure 1).
- MFC Minimum frontal carinal distance: minimum distance between the frontal carinae, measured with the head in full-face, dorsal view (Figure 1).
- EW Eye width: maximum width of compound eye, measured along its short axis, in an oblique dorso-lateral view of the head.
- SL Scape length: length of the first antennal segment, excluding the radicle.
- LF1 Length of first funicular segment: maximum measurable length of the first funicular segment (pedicel), excluding its basal articulation.
- LF2 Length of second funicular segment: maximum measurable length of the second funicular segment.
- FL Forefemur length: maximum measurable length of the forefemur, measured in posterior view (Figure 3).
- FW Forefemur width: maximum measurable width of the forefemur, measured from the same view as FL, at right angles to the line of measurement of FL (Figure 3).
- DPL Diagonal length of the propodeum: length of the propodeum, measured in lateral view along a diagonal line drawn from the metapleural lobe to the

- metanotal groove (Figure 2).¹
- BF Length of the basal (= dorsal) face of the propodeum, measured in lateral view from the metanotal groove to the point on the surface of the propodeum which is maximally distant from the diagonal propodeal line (Figure 2).
- DF Length of the declivitous face of the propodeum, measured in lateral view from the metapleural lobe to the point on the surface of the propodeum which is maximally distant from the diagonal propodeal line (Figure 2).
- MP Depth of metanotal groove ("mesopropodeal impression"), measured in lateral view from the bottom of the metanotal groove to a line drawn across the dorsal surface of the mesonotum and propodeum.
- PL Petiole length: length of the petiole, measured in lateral view from the lateral flanges of the anterior peduncle to the posterior margin of the petiole (Figure 4).
- PND Petiolar node distance: distance from the anterior margin of petiole to the maximum height of the node measured from the same view as PL and along the same line of measurement (Figure 4).
- PH Petiole height: maximum height of the petiole, measured in lateral view at right angles to PL, but excluding the anteroventral process (Figure 4).
- PPL Postpetiole length: length of the postpetiole, measured in lateral view, from the anterior peduncle (of the postpetiole) to the point of contact with the fourth abdominal tergite (Figure 4).
- DPW Dorsal petiolar width: maximum width of the petiole, measured in dorsal view.
- PPW Dorsal postpetiolar width: maximum width of the postpetiole, measured in dorsal view.

Indices calculated from the preceding measurements include the following ratios:

- CI Cephalic index: HW/HL
- OI Ocular index: EW/EL
- REL Relative eye length: EL/HL
- REL2 Relative eye length, using HW: EL/HW
- OOI Oculo-ocellar index: OOD/OD
- VI Vertex width index: VW/HW
- FCI Frontal carinal index: MFC/HW
- CDI Clypeal distance index: CD/HL
- SI Scape index: SL/HW
- SI2 Scape index, using EL: SL/EL
- SI3 Scape index, using LF2: $SL/LF2$
- FI Forefemur index: FW/FL
- PDI Propodeal index: BF/DF

¹In *Pseudomyrmex* DPL is more appropriate than WL (Weber's length of the mesosoma (alitrunk), taken from the anterior pronotal margin to the metapleural lobe) since the articulation of the pronotum with the mesothorax renders the measurement of WL imprecise.



Figures 1-4. Views of a generalized *Pseudomyrmex* worker, illustrating some measurements. 1. Frontal view of head. CD, clypeal distance; EL, eye length; HL, head length; HW, head width; MFC, minimum distance between frontal carinae; OD, ocellar distance; OOD, oculo-ocular distance; VW, vertex width. 2. Lateral view of propodeum. BF, length of basal (= dorsal) face of propodeum; DF, length of declivitous face of propodeum; DPL, diagonal propodeal length. 3. Posterior view of forefemur. FL, forefemur length; FW, forefemur width. 4. Lateral view of petiole and postpetiole. PH, petiolar height; PND, petiolar node distance; PL, petiolar length; PPL, postpetiolar length.

MPI	Metanotal index: MP/HW
NI	Petiole node index: PND/PL
PLI	Petiole length index: PH/PL
PLI2	Petiole length index, using PPL: PPL/PL
PHI	Petiole height index, using PPL: PH/PPL
PWI	Petiole width index: DPW/PL
PWI2	Petiole width index, using PPW: DPW/PPW
PPWI	Postpetiole width index: PPW/PPL
PPWI2	Postpetiole width index, using HW: PPW/HW

SYNOPSIS

Workers of *Pseudomyrmex* may be recognized by their large compound eyes (REL 0.39–0.61), closely set frontal carinae and antennal insertions (FCI 0.01–0.07), and short scapes (SI 0.40–0.51). There is a distinct postpetiole and a well-developed sting.

Among the Nearctic fauna I recognize three species groups, whose workers may be diagnosed as follows (the *gracilis* group preceding the other two on the basis of its distinctive size and habitus):

gracilis group (see also Kempf 1958)

Large black, orange, or bicolored species (HW > 1.20), with broad head, large eyes (REL > 0.50), and relatively long scapes (SI 0.50); frontal carinae subcontiguous; lateral margins of pronotum angled; petiole usually long, with a distinct anterior peduncle. Erect pilosity abundant on body and appendages, including propodeum, scapes, and legs.

elongatus group

Small, brown species (HW 0.56–0.75), with elongate head (CI < 0.80) and long eyes (REL 0.47–0.58); scapes relatively short (SI 0.45); frontal carinae subcontiguous; lateral margins of pronotum rounded; petiole very short, without a distinct anterior peduncle (PLI 0.65–0.91; PWI 0.55–0.74). Erect pilosity present on most parts of body, including mesonotum and propodeum.

pallidus group

Small yellow, orange or brown species (HW 0.55–1.04), with elongate head (CI 0.75–0.91); scapes usually short; frontal carinae contiguous or subcontiguous; lateral margins of pronotum rounded; petiole usually slender, with an anterior peduncle (PLI 0.43–0.69; PWI 0.38–0.65). Erect pilosity scarce, lacking on the mesonotum and propodeum.

SYNONYMIC LIST OF NEARCTIC *PSEUDOMYRMEX* SPECIES

gracilis group

P. mexicanus Roger, 1863

elongatus group

P. elongatus Mayr, 1870

= *P. tandem* Forel, 1906

P. cubaensis Forel, 1901, *stat. nov.*

pallidus group*P. apache* Creighton, 1952*P. brunneus* F. Smith² 1877= *P. nigritus* Enzmann, 1945, *syn. nov.**P. ejectus* F. Smith, 1858*P. leptosus* *sp. nov.**P. pallidus* F. Smith, 1855*P. seminole* *sp. nov.**P. simplex* F. Smith, 1877= *P. delicatulus* Forel, 1899, *syn. nov.*= *P. capperi* Forel, 1899, *syn. nov.*= *P. panamensis* Forel, 1899, *syn. nov.*= *P. vittatus* Forel, 1912, *syn. nov.***Key to species: workers (excluding *P. leptosus* new species of which the worker is unknown)**

- 1 (a) Erect hairs conspicuous on most parts of body, including mesonotum and propodeum 2
- (b) Erect pilosity very sparse, lacking on mesonotum and (nearly always) propodeum 4
- 2 (a) Large, bicolored orange and black species (HW > 1.40); head approximately as wide as long (CI > 0.95); petiole with a long anterior peduncle (PLI < 0.55) (Figure 12); Florida, Texas south to Panama *P. mexicanus* Roger, p. 225
- (b) Small, unicolored brown species (HW < 0.80); head notably longer than wide (CI < 0.80); petiole short (PLI > 0.60) (*e.g.*, Figure 6) 3
- 3 (a) Larger species (HW ≥ 0.64), with shorter eyes (REL2 0.63–0.73), and a lower, thinner petiole (PLI 0.65–0.78) (Figures 5,6); Florida, West Indies *P. cubaensis* Forel, p. 226
- (b) Smaller species (HW ≤ 0.64), with longer eyes (REL2 0.73–0.82), and a higher, broader petiole (PLI 0.76–0.91) (Figures 7,8); Florida, Texas south to Colombia *P. elongatus* Mayr, p. 227
- 4 (a) Head and gaster usually dark brown; small species (HW < 0.82), with a deep, wide metanotal groove (*e.g.*, Figure 14) (MPI 0.046–0.097); basal face of propodeum generally shorter than declivitous face (PDI 0.56–1.07) 5
- (b) Head and gaster golden yellow to orange-brown (fourth abdominal tergite may have darker fuscous patches); variable in size (HW 0.55–1.04), metanotal groove usually relatively shallow (*e.g.*, Figure 43) (MPI 0.005–0.054); if metanotal groove very deep (MPI ≥ 0.046), then basal face of propodeum notably longer than declivitous face (PDI ≥ 1.10) 6
- 5 (a) Basal face of propodeum about one half to three quarters the length of the declivitous face (PDI 0.56–0.75) (Figure 13); petiole with long anterior peduncle, the node somewhat displaced posteriorly (NI 0.57–0.65); petiole and postpetiole very broad (PWI 0.54–0.65; PPWI 1.26–1.54) (Figure 15);

²Occurring no farther north than northern Mexico

- Mexico** *P. brunneus* F. Smith, p. 231
- (b) Basal face of propodeum longer (PDI 0.70–1.07) (Figure 14); summit of petiolar node in a more anterior position (NI 0.48–0.60); petiole and postpetiole less broad (PWI 0.40–0.52; PPWI 0.93–1.25) (Figure 16); southeastern United States, south to Costa Rica *P. ejectus* F. Smith, p. 231
- 6 (a) Fourth abdominal tergite (first “gastric” tergite) smooth and strongly shining, more or less devoid of appressed pubescence; vertex of head smooth and shining; broad forefemur (FI 0.45–0.52); small species, with relatively long eyes (HW 0.55–0.74; OI 0.49–0.55; REL 0.52–0.61); Florida, West Indies, Mexico south to Brazil *P. simplex* F. Smith, p. 238
- (b) Fourth abdominal tergite subopaque, covered with a (usually dense) mat of fine appressed pubescence; vertex of head at least slightly coriarius, weakly shining to subopaque; longer forefemur (FI \leq 0.45); generally larger species, with relatively shorter eyes (HW 0.68–1.04; OI 0.54–0.65; REL 0.39–0.54) 7
- 7 (a) Eyes short (REL 0.39–0.44); scapes relatively long, subequal to eye length (SI2 0.90–1.00); median (protruded) portion of anterior clypeal margin laterally rounded (Figure 9); frontal carinae relatively well-separated, the minimum distance between them subequal to the basal width of the scape (MFC 0.033–0.066, FCI 0.034–0.070); southwestern United States, northern Mexico *P. apache* Creighton, p. 229
- (b) Eyes longer (REL 0.43–0.54); scapes notably shorter than eye length (SI2 0.68–0.85); median portion of anterior clypeal margin laterally angulate (e.g., Figure 42); frontal carinae variable, often more closely contiguous so that the minimum distance between them is notably less than the basal width of the scape (MFC 0.011–0.042, FCI 0.015–0.047) 8
- 8 (a) Larger species (HW 0.87–0.96); frontal carinae relatively well-separated (MFC 0.029–0.042, FCI 0.031–0.047); eyes relatively short (REL 0.43–0.48); median portion of anterior clypeal margin weakly angulate, thus appearing tridentate (Figure 44); Gulf states, Mexico *P. seminole* sp. nov., p. 237
- (b) Smaller species (HW 0.68–0.89); frontal carinae more closely contiguous (MFC 0.011–0.024, FCI 0.015–0.033); eyes averaging a little longer (REL 0.45–0.54); median portion of anterior clypeal margin usually straight (Figure 42); southern United States, south to Costa Rica *P. pallidus* F. Smith, p. 234

Key to species: queens

- 1 (a) Large, bicolored orange and black species (HW $>$ 1.45); erect pilosity abundant on most parts of body, including propodeum; petiole with a long anterior peduncle (PLI $<$ 0.55); Florida, Texas south to Panama *P. mexicanus* Roger, p. 225

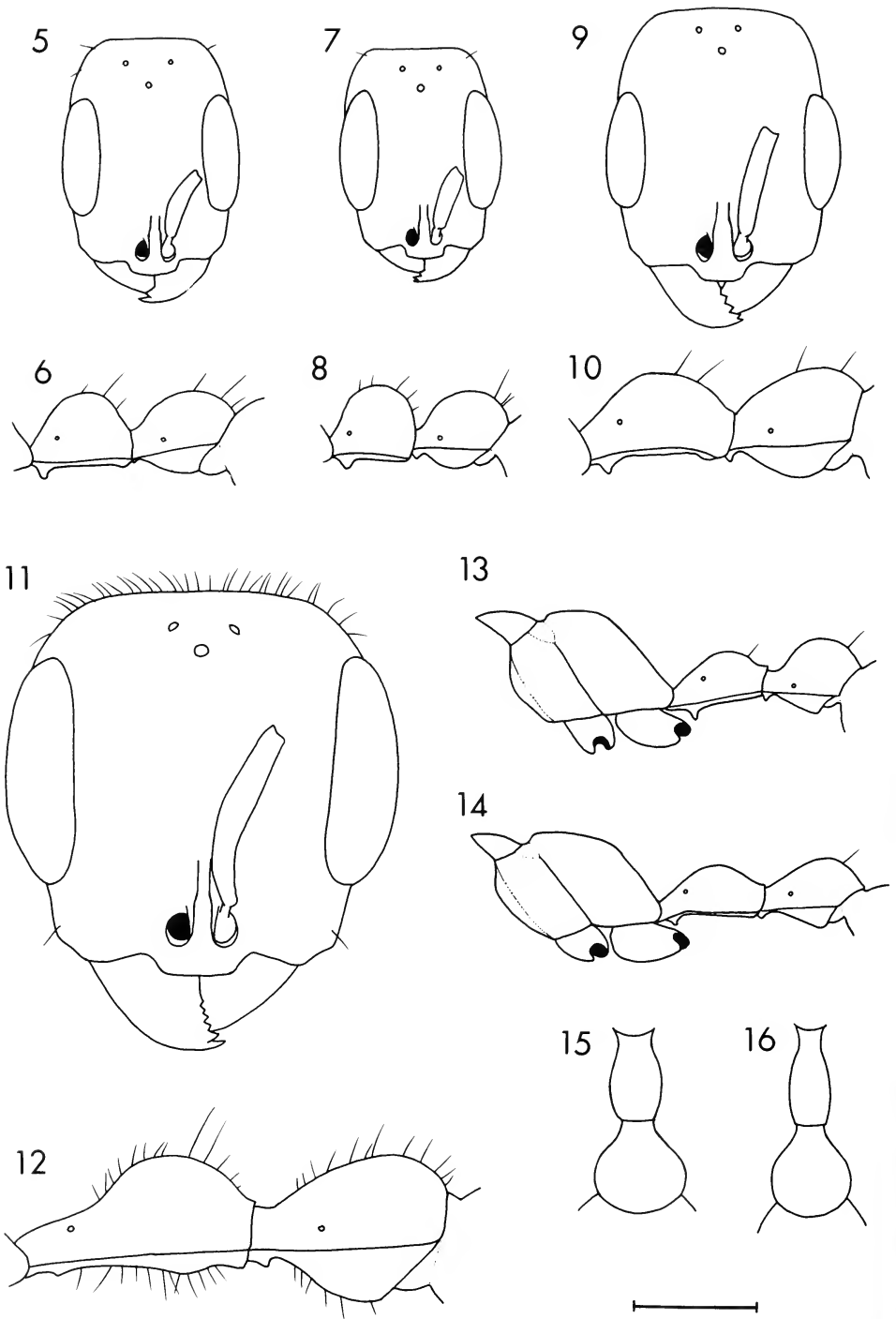
- (b) Smaller species (HW < 1.10); *either* petiole very short and without a conspicuous peduncle (PLI > 0.55), *or* erect pilosity sparse (lacking on propodeum) 2
- 2 (a) Head densely punctate, and more than 1.5 times as long as wide (CI 0.57–0.64); petiole short (PLI 0.58–0.76); usually some erect hairs on the propodeum 3
- (b) Head varying from finely punctate, to coriarius, to smooth and shining, and no more than 1.5 times as long as wide (CI 0.66–0.86); petiole relatively long (PLI 0.43–0.58); propodeum essentially lacking erect setae 4
- 3 (a) Larger species (HW 0.65–0.72, in a sample of 10 queens); eye length less than one half head length (REL 0.43–0.47, n = 10); petiole moderately long (PLI 0.58–0.67, n = 10); Florida, West Indies
P. cubaensis Forel, p. 226
- (b) Smaller species (HW 0.56–0.58, n = 5); eye length about one half head length (REL 0.48–0.53); petiole short (PLI 0.66–0.76, n = 5); Florida, Texas south to Colombia
P. elongatus Mayr, p. 227
- 4 (a) Head and gaster dark brown; small species (HW 0.62–0.75); frontal carinae closely contiguous (MFC 0.010–0.018, FCI 0.015–0.026); petiole long and slender, more than twice as long as high (PLI 0.43–0.48) 5
- (b) Head and gaster golden yellow to orange-brown (small fuscous patches may be present on gaster); mostly larger species (HW 0.57–1.03); if HW < 0.80, then *either* the frontal carinae tend to be less closely contiguous (MFC 0.016–0.035; FCI 0.022–0.046) *and/or* the petiole is relatively short (PLI 0.48–0.58) 6
- 5 (a) Petiole and postpetiole relatively broad, the latter about 1.25 times as wide as long (PHI 0.72, PWI 0.48, PPWI 1.26, in single specimen examined); frons opaque, fine punctures more or less obscured by coarse coriarius sculpture; Mexico
P. brunneus F. Smith, p. 231
- (b) Petiole and postpetiole less broad, the latter about as wide as long (PHI 0.57–0.67, PWI 0.42–0.48, PPWI 1.00–1.12; n = 13); frons usually weakly shining, distinctly punctulate on a weaker coriarius background; southeastern United States south to Costa Rica
P. ejectus F. Smith, p. 231
- 6 (a) Fourth abdominal tergite (first “gastric” tergite) smooth and shining, appressed pubescence inconspicuous, hairs (if present) separated by about their lengths; vertex of head usually smooth and shining, with scattered fine punctures; small species (HW 0.57–0.75), with contiguous frontal carinae (MFC 0.008–0.021; FCI 0.014–0.029) and relatively long eyes (REL2 0.65–0.80); SI2 0.52–0.68 (n = 17 for this and preceding measurements); Florida, West Indies, Mexico south to Brazil
P. simplex F. Smith, p. 238
- (b) Fourth abdominal tergite weakly shining to subopaque, with a (usually dense) mat of appressed pubescence; *either* vertex of head weakly shining to subopaque, and coriarius with punctures, *or* SL about three-quarters of EL (SI2 0.75–0.77); generally larger species (HW 0.66–1.03); frontal carinae less closely contiguous (MFC 0.016–0.095; FCI 0.022–0.094); eyes

- usually shorter (REL2 0.52–0.71); SI2 0.64–0.95 (n = 61) 7
- 7 (a) Larger species (HW 0.85–1.03, HL 1.28–1.46); frontal carinae relatively well separated (MFC 0.053–0.095; FCI 0.052–0.094); eyes relatively short (REL2 0.52–0.58) 8
- (b) Smaller species (HW 0.66–0.92, HL 0.82–1.15); frontal carinae more closely contiguous (MFC 0.016–0.035; FCI 0.022–0.046); eyes longer (REL2 0.59–0.71) 9
- 8 (a) Eye length (EL) more than 1.25 times scape length (SI2 0.70–0.80; n = 10); petiole longer, with a more slender anterior peduncle (PLI 0.43–0.49, PWI 0.41–0.51; n = 10); Gulf states, Mexico *P. seminole* sp. nov., p. 237
- (b) Eye length less than 1.20 times scape length (SI2 0.85–0.95; n = 10); petiole shorter and broader (PLI 0.49–0.57, PWI 0.54–0.60; n = 10); southwestern United States, northern Mexico *P. apache* Creighton, p. 229
- 9 (a) Head, especially upper half, smooth and shining, with scattered fine punctures (Figure 34); occipital margin broadly rounded, so that VI 0.68–0.75 (n = 11); small species (HW 0.67–0.70; n = 11); Florida *P. leptosus* sp. nov., p. 233
- (b) Head coriarius and weakly shining, punctures coarser (Figure 36); lateral margins of occiput more sharply rounded, giving head a more quadrate shape (VI 0.71–0.88; n = 30); larger species, on average (HW 0.66–0.92; n = 30); southern United States, south to Costa Rica *P. pallidus* F. Smith, p. 234

Key to species: males (excluding *P. brunneus* F. Smith, of which the male is unknown).

- 1 (a) Larger species (HW > 1.30); head wider than long (CI > 1.05); Florida, Texas south to Panama *P. mexicanus* Roger, p. 225
- (b) Smaller species (HW < 1.00); head longer than wide (CI < 0.98) 2
- 2 (a) Posterior margin of pygidium (eighth abdominal tergite) convex and pointing posteroventrally (Figure 17); posterior margin of hypopygium straight or broadly convex 3
- (b) Posterior margin of pygidium recurved forward, and forming a pocket which opens anteroventrally (Figure 18); posterior margin of hypopygium concave 5
- 3 (a) Head elongate (CI < 0.80), upper half densely punctate; eyes relatively long, EL about three-quarters of head width (REL2 0.71–0.83) 4
- (b) Head broader (CI > 0.80) and not densely punctate; eyes shorter, EL about one-half head width (REL2 0.50–0.57); southwestern United States, northern Mexico *P. apache* Creighton, p. 229
- 4 (a) Larger species, with very elongate head (HW 0.76–0.82, CI 0.65–0.71, in a sample of 6 males); eyes short relative to head length (REL 0.49–0.51; n = 6); SI 0.26–0.28 (n = 6); in dorsal view, outer margin of paramere indented distally (Figure 25); Florida, West Indies *P. cubensis* Forel, p. 226

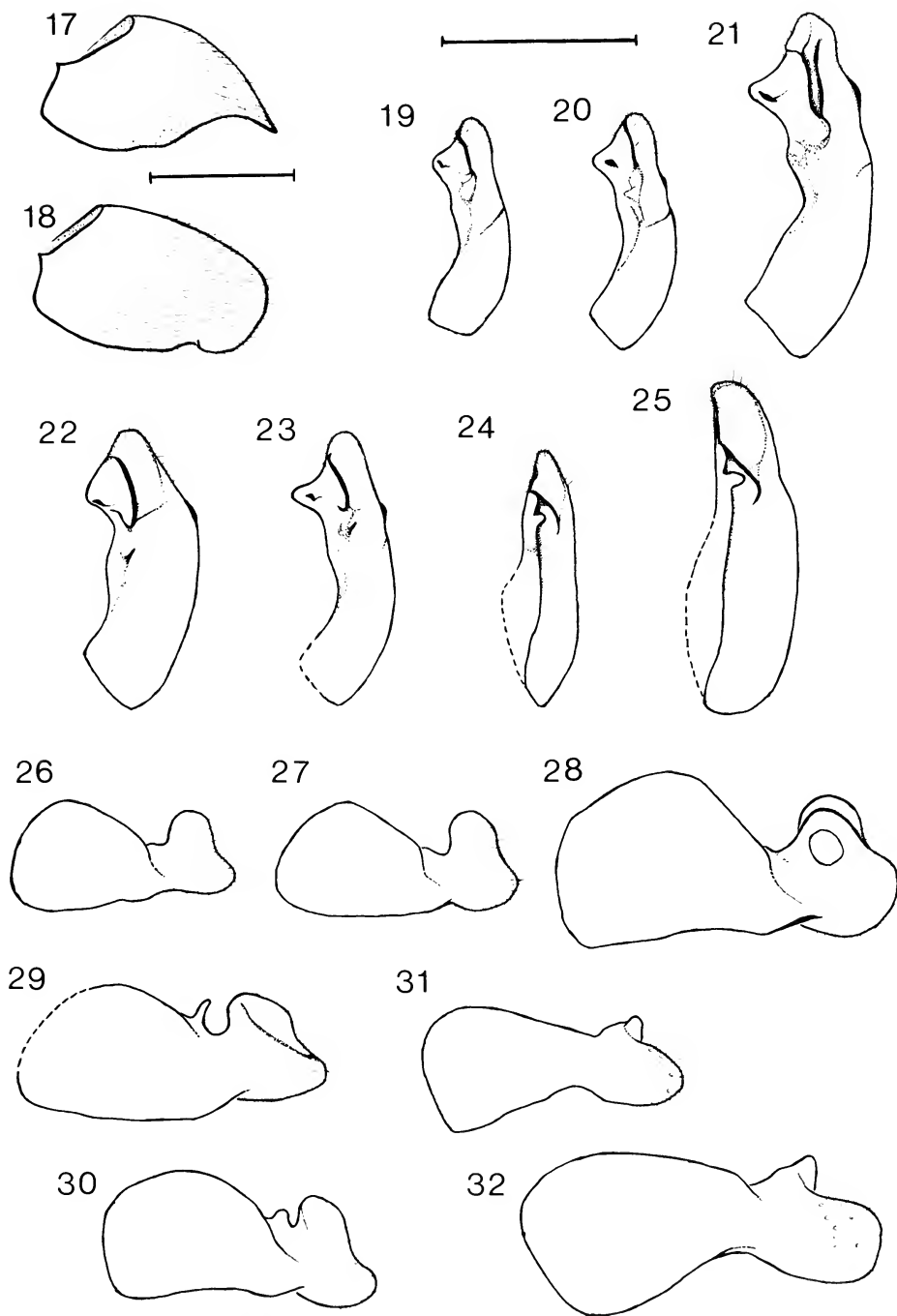
- (b) Smaller species, with less elongate head (HW 0.59-0.62, CI 0.69-0.76; $n = 7$); eyes relatively longer (REL 0.55-0.58; $n = 7$); SI 0.22-0.25 ($n = 7$); in dorsal view, outer margin of the paramere not notably indented (Figure 24); Florida, Texas south to Colombia *P. elongatus* Mayr, p. 227
- 5 (a) In lateral view, caudal end of paramere consisting of a large dorsal lobe preceded by a small, dorsal spine (Figures 29, 30); *either* forefemur rather broad ($FI \geq 0.36$) *or* posterior margin of hypopygium with a median, ventral protuberance 6
- (b) In lateral view, caudal end of paramere consisting of a dorsal lobe, unpreceded by a smaller spine (Figures 26-28); forefemur relatively elongate ($FI \leq 0.36$); posterior margin of hypopygium lacking a distinct ventral protuberance 7
- 6 (a) Forefemur relatively elongate (FI 0.30-0.36; $n = 7$); in dorsal view, inner caudal margin of paramere strongly concave (Figure 23); posterior margin of hypopygium with a median, ventral protuberance; southeastern United States south to Costa Rica *P. ejectus* F. Smith, p. 231
- (b) Forefemur broader (FI 0.36-0.51; $n = 11$); in dorsal view, inner caudal margin of paramere more or less straight (Figure 22); posterior margin of hypopygium without a distinct ventral protuberance; Florida, West Indies, Mexico south to Brazil *P. simplex* F. Smith, p. 238
- 7 (a) Larger species (HW 0.81-0.92; $n = 6$); eyes relatively shorter (REL 0.56-0.59; $n = 6$); dorsal lobe of paramere much broadened and bicarinate along its dorsal margin, and invaginated below the margin so that in lateral view a distinct lunule is visible (Figure 28); Gulf states, Mexico *P. seminole* sp. nov., p. 237
- (b) Smaller species (HW 0.61-0.84; $n = 17$); eyes relatively longer (REL 0.58-0.71; $n = 17$); dorsal lobe of paramere consisting of a thin lamella, without a lunule (Figures 26, 27) 8
- 8 (a) Larger species (HW 0.67-0.84; $n = 12$); scape generally subequal in length to second funicular segment (SI3 0.80-1.13; $n = 12$); in dorsal view, outer margin of the paramere indented distally, posterior to a small but distinct protuberance (Figure 20); southern United States south to Costa Rica *P. pallidus* F. Smith, p. 234
- (b) Smaller species (HW 0.61-0.68; $n = 5$); scape length exceeding length of second funicular segment (SI3 1.11-1.25; $n = 5$); in dorsal view, outer margin of the paramere lacking a protuberance and showing no distinct distal indentation (Figure 19); Florida *P. leptosus* sp. nov., p. 233



Figures 5-12. *Pseudomyrmex* workers: frontal views of head, and lateral views of petiole and postpetiole. 5,6. *P. cubaensis* (Florida); 7,8. *P. elongatus* (Florida); 9,10. *P. apache* (Arizona); 11,12. *P. mexicanus* (Texas).

Figures 13-16. *Pseudomyrmex* workers. 13, 14, lateral views of mesothorax, propodeum, petiole, and postpetiole. 15, 16, dorsal views of petiole and postpetiole. 13,15 *P. brunneus* (Mexico); 14,16. *P. ejectus* (Mexico).

All drawings to same scale; scale line = 0.5 mm.



Figures 17,18. *Pseudomyrmex* males: lateral views of eighth abdominal tergite (pygidium). 17, *P. apache* (Texas); 18, *P. seminole* (Florida). Scale line = 0.5mm.

Figures 19-32. Left parameres of *Pseudomyrmex* males. 19-25, dorsal views, with caudal end uppermost; 26-32, lateral views, with caudal end to the right. 19,26, *P. leptosus* (paratype, Florida); 20,27, *P. pallidus* (Florida); 21,28, *P. seminole* (paratype, Florida); 22,29, *P. simplex* (Florida); 23,30, *P. ejectus* (Texas); 24,31, *P. elongatus* (Florida); 25,32, *P. cubaensis* (Florida). Scale line = 0.5 mm.

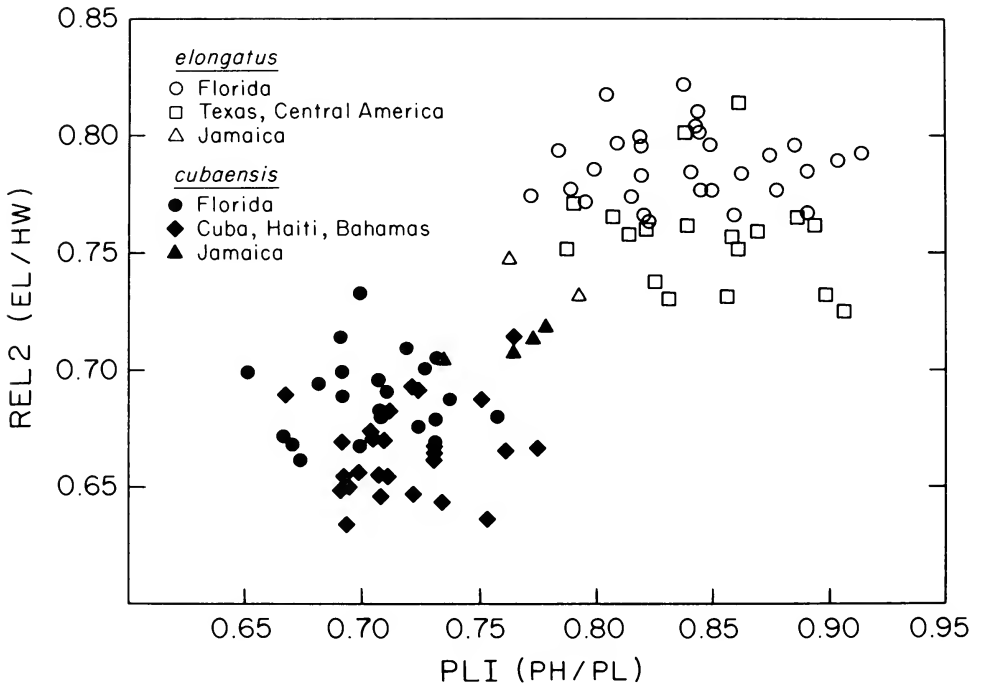
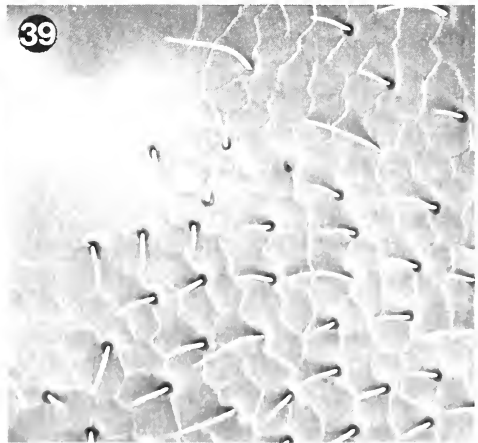
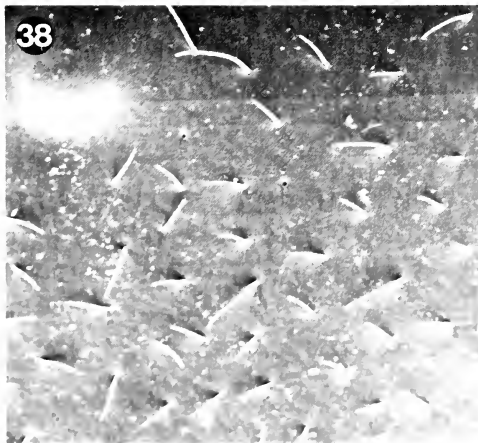
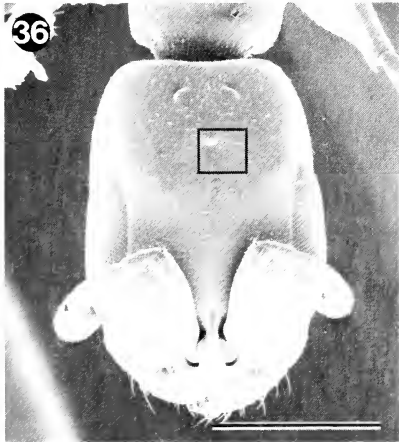
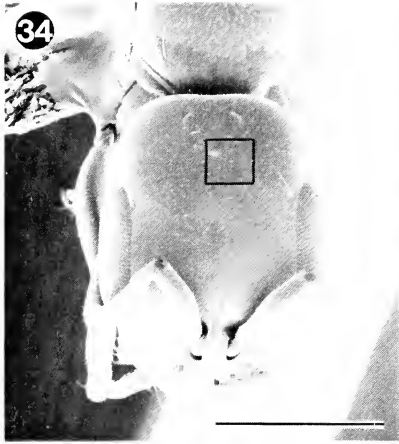
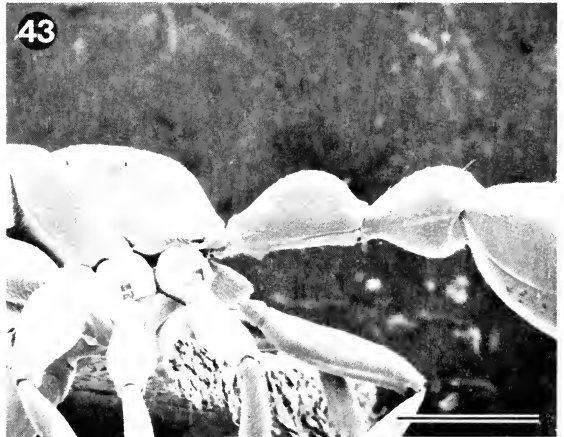
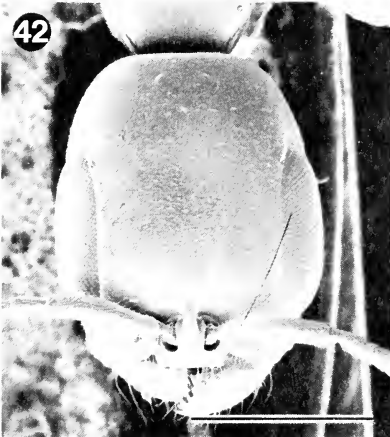
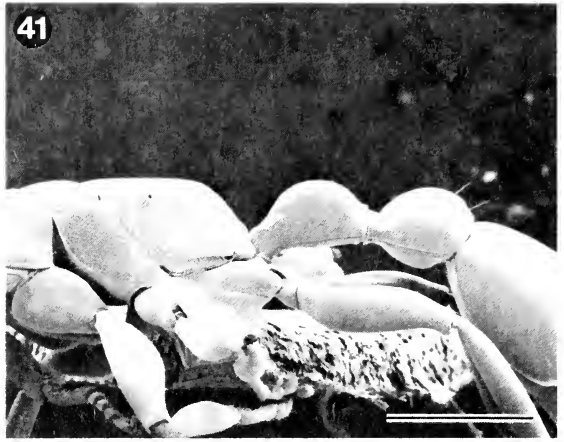
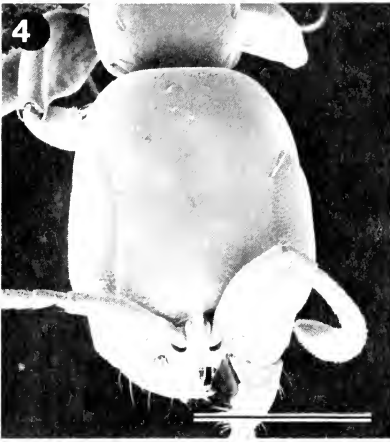


Figure 33. Plot of relative eye length (REL2) and petiole length index (PLI) in workers of *Pseudomyrmex cubaensis* and *P. elongatus*.



Figures 34-39. *Pseudomyrmex* queens. 34, 36, dorsal views of head; 35, 37, lateral views of mesosoma (part), petiole, postpetiole, and gaster (part); 38-39, close-up views of head sculpture, from insets. 34,35,38, *P. leptosus* (holotype, Florida); 36,37,39, *P. pallidus* (Florida). Scale lines = 0.5 mm.



Figures 40-45. *Pseudomyrmex* workers. 40, 42, 44, dorsal views of head; 41, 43, 45, lateral views of mesosoma (part), petiole, postpetiole, and gaster (part). 40,41, *P. simplex* (Florida); 42,43, *P. pallidus* (Florida); 44,45, *P. seminole* (holotype, Florida). Scale lines = 0.5 mm.

SPECIES ACCOUNTS

gracilis group*Pseudomyrmex mexicanus* Roger

(Figs. 11, 12)

Pseudomyrma mexicana Roger, 1863, p. 178. Syntype worker(s), Mexico (not in MNHU) [Not examined].*Pseudomyrma gracilis* var. *mexicana* Roger; Wheeler, 1901, p. 204.*Pseudomyrma gracilis* var. *mexicana* Roger; Wheeler, 1908, p. 421.*Pseudomyrma gracilis mexicana* Roger; Mitchell & Pierce, 1912, p. 69.*Pseudomyrma gracilis* var. *mexicana* Roger; Wheeler & Bailey, 1920, pp. 259, 262. [Description of larva, and contents of food pellets].*Pseudomyrma gracilis* subsp. *mexicana* Roger; Wheeler, 1942, pp. 166, 167.*Pseudomyrma gracilis mexicana* Roger; Creighton, 1950, p. 80.*Pseudomyrmex mexicanus* Roger; Whitcomb *et al.*, 1972, pp. 31-33.

Worker Measurements ($n = 13$): HL 1.50–1.72, HW 1.53–1.70, MFC 0.036–0.051, CI 0.98–1.02, OI 0.49–0.54, REL 0.54–0.60, REL2 0.54–0.60, OOI (–0.19)–(+0.39), VI 0.71–0.81, FCI 0.023–0.033, SI 0.47–0.51, SI2 0.80–0.92, FI 0.37–0.41, PDI 1.03–1.32, MPI 0.058–0.073, NI 0.62–0.71, PLI 0.46–0.51, PWI 0.41–0.47, PPWI 0.94–1.12.

Worker Diagnosis.— Immediately distinguishable from all other Nearctic *Pseudomyrmex* by its large size (worker HW > 1.40) and bicolored, orange and black markings. Head broad (CI 1.00), frontal carinae moderately well separated (MFC 0.04), eyes large (REL 0.58); occipital margin convex to flat, in full-face, dorsal view; pronotum laterally margined; metanotal groove distinct; basal face of propodeum rounding into declivitous face, and not distinctly differentiated from it; petiole and postpetiole elongate, the former with a well-developed anterior peduncle. Integument mostly subopaque, due to fine coriaceous or punctulate sculpture. Appressed and erect hairs common on most parts of the body, including mesonotum, propodeum, legs, and scapes. Gaster and most of head black; mesosoma (= alitrunk), petiole, and postpetiole orange, with varying amounts of black infuscation (commonly the pronotum is orange, while the mesonotum and propodeum are dark).

Comments.— I have been unable to locate type material of *P. mexicanus* (not present in MNHU, according to F. Koch, *in litt.*). Application of this name to the Nearctic representative of the *gracilis* group is based upon the original description and the type locality. *P. mexicanus* belongs to a complex of closely related forms of uncertain taxonomic status, distinguished mainly on the basis of color (the so-called *gracilis* complex, within the *Pseudomyrmex gracilis* group). These taxa are often listed as subspecies of *gracilis*, despite the fact that some forms are broadly sympatric. *P. mexicanus* is similar to the Central American taxon, *bicolor* Guerin; the latter is ostensibly darker on average, with a more slender petiole. However, the members of the *gracilis* complex exhibit notable variation in color patterns and in the shape of the petiole. A thorough systematic analysis is needed to disentangle the intra- and inter-specific components of this variation. The occurrence of modal color patterns and transitional forms suggests that some of the taxa are incompletely isolated (semispecies).

Biology.— *P. mexicanus* nests in dead or cavity-ridden branches in a wide variety of trees, shrubs, and herbs. Museum records include nests from the following plants: *Baccharis*, *Cladium*, *Peperomia*, *Prosopis*, *Rhizophora*, and *Salix*. Apparently introduced into Florida in recent times (first collected in 1960), *P. mexicanus* is now common in the southern half of the state, where it occurs in hardwood hammocks, mangrove, and old field second growth habitats. Whitcomb *et al.* (1972) provide notes on nesting and feeding behavior in Florida.

Material Examined (GCW, LACM, MCZ, PSW, UCD, USNM).—

FLORIDA: *Collier Co.*: Collier-Seminole St. Pk. (P. S. Ward); *Dade Co.*: Hialeah (C. Stegmaier); Homestead A.F.B. (G. C. & J. Wheeler); Long Pine Key (G. C. & J. Wheeler); Mahogany Hammock, Everglades Natl. Pk. (R. Wagner; G. C. & J. Wheeler); Old Flamingo Rd., Everglades Natl. Pk., 10 m (P. S. Ward); *Indian River Co.*: Vero Beach (L. & C. W. O'Brien); *Monroe Co.*: Bear Lake Trail, near Flamingo, Everglades Natl. Pk. (G. C. & J. Wheeler); John Pennekamp State Pk. < 5 m (P. S. Ward).

TEXAS: *Aransas Co.*: Goose I. St. Pk., 5 m (P. S. Ward); *Brazoria Co.*: 4 mi SW West Columbia (P. S. Ward); *Cameron Co.*: 5 mi W Boca Chica (G. C. & J. Wheeler); 10 mi W Boca Chica (W. S. Creighton); Brownsville (Darlington; Jones & Pratt; D. J. & J. N. Knull; Lattimore & Bottimer; McMillan; C. H. T. Townsend); Harlingen (W. Buren); Laguna Madre, 25 mi SE Harlingen (D. E. Hardy); no specific locality (Dreyer; D. J. & J. N. Knull); *Hidalgo Co.*: Bentsen Rio Grande St. Pk. (E. E. Grissell & A. S. Menke; P. S. Ward); Mission (P. C. Avery); Pharr; Santa Ana Refuge (P. S. Ward); no specific locality (D. J. & J. N. Knull); *Kenedy Co.*: 27°10'N, 97°40'W (J. E. Gillaspay); *Kleberg Co.*: Kingsville (J. E. Gillaspay); *Live Oak Co.*: 4 mi S George West (R. Snelling); *Nueces Co.*: Corpus Christi (R. A. Cushman; Jones & Pratt); *Victoria Co.*: Victoria (J. D. Mitchell).

Other material, tentatively identified as *P. mexicanus*, from Mexico, Guatemala, Nicaragua, Costa Rica, Panama and Jamaica.

elongatus group*Pseudomyrmex cubaensis* Forel stat. nov.

(Figs. 5, 6, 25, 32)

Pseudomyrma elongata var. *cubaensis* Forel, 1901, p. 342. Holotype (unique syntype) worker, Bahia Honda, Cuba (MHN) [Examined].

Pseudomyrma elongata; Wheeler (nec Mayr), 1905, pp. 85-87 (partim).

Pseudomyrma elongata var. *cubaensis* Forel; Forel, 1913, p. 215 [Description of queen].

Pseudomyrma elongata var. *cubaensis* Forel; Wheeler, 1913a, pp. 484-485.

Pseudomyrma elongata var. *cubaensis* Forel; Wheeler & Mann, 1914, p. 18.

Pseudomyrma elongata var. *cubaensis* Forel; Mann, 1920, p. 405

Pseudomyrma elongata; Wheeler & Bailey (nec Mayr), 1920, pp. 260, 265 [Description of larva, and contents of food pellets].

Pseudomyrma elongata; Wheeler (nec Mayr), 1932, p. 4 (partim).

Pseudomyrma elongata; Wheeler (nec Mayr), 1942, p. 165.

Pseudomyrma elongata; Creighton (nec Mayr), 1950, pp. 79-80 (partim).

Pseudomyrmex elongata; Creighton (nec Mayr), 1955, pp. 17-20 (partim).

Pseudomyrmex elongatus; Wheeler & Wheeler (nec Mayr), 1956, p. 384 [Description of larva].

Worker Measurements ($n = 21$, except for HL, HW, CI, REL, REL2, and PLI, where $n = 52$): HL 0.84–1.05, HW 0.64–0.75, MFC 0.017–0.029, CI 0.69–0.77, OI 0.52–0.58, REL 0.47–0.51, REL2 0.63–0.73, OOI 0.41–0.95, VI 0.74–0.83, FCI 0.024–0.044, SI 0.44–0.48, SI2 0.64–0.74, FI 0.42–0.48, PDI 1.09–1.44, MPI 0.038–0.084, NI 0.53–0.63, PLI 0.65–0.78, PWI 0.55–0.69, PPWI 1.01–1.25.

Worker Diagnosis.— A small, brown species with elongate head (HW 0.64–0.75, CI 0.69–0.77) and with erect pilosity on the mesonotum and propodeum. Very similar to *P. elongatus* Mayr (q.v.), except averaging larger, with relatively short eyes (REL2 0.63–0.73) and a longer petiole and postpetiole (PLI 0.65–0.78). Head punctate, the punctures maximally separated by about their diameters.

Comments.— Originally described as a variety of *P. elongatus*, *P. cubaensis* was synonymized with the former by Creighton (1955, p. 18). However it appears to be consistently distinct from the smaller *elongatus*-like form with which occurs sympatrically in south Florida. The most important differences are in the relative length of the eye and the shape of the petiole. A two-dimensional plot of REL2 and PLI cleanly separates all Floridian and most other material into two taxa (Figure 33). In Jamaica the two forms are less distinct. It is possible that *P. elongatus* and *P. cubaensis* represent a remnant circular Rassenkreis stretching around the

Gulf of Mexico, with intermediate populations in Jamaica.

Apart from the differences in eye length and petiole shape, *P. cubaensis* also tends to have a broader head, narrower forefemur (FI 0.42–0.48), longer postpetiole (PPWI 1.01–1.25), and fewer (but longer) erect setae on the petiole, postpetiole, and fourth abdominal tergite. The body sculpture and appressed pubescence is lighter than in Florida *P. elongatus*, producing a shinier appearance, particularly on the occiput, propleuron, petiole, and postpetiole. (Elsewhere *P. elongatus* may have an equally shiny integument, e.g. in Texas.)

Differences between queens and males of the two species are given in the respective keys.

Biology.— In Florida, I have collected *P. cubaensis* in dead twigs of *Rhizophora mangle* and *Conocarpus erectus*. There are museum records of nests in *Tillandsia* (Florida) and *Cladium* (Bahamas), and of workers foraging on *Ficus aurea*, mangrove, sea grape, and acacia. Wheeler's (1905) records of Bahamaian "*elongatus*" in culms of *Uniola* and *Cladium* and in hollow twigs of gum mastic, sea grape, and buttonwood, refer in part to *P. cubaensis* (see also discussion of *Pseudomyrmex subater* Wheeler & Mann under *P. elongatus*).

Material Examined (LACM, MCZ, PSW, UCD, USNM).—

FLORIDA: *Collier Co.*: Collier-Seminole St. Pk. (P. S. Ward); Marco (W. T. Davis); *Dade Co.*: Biscayne Bay (Slosson); Cards Point (W. M. Wheeler); Long Pine Key (W. M. Wheeler); Miami Beach (W. E. Brown; A. C. Cole); Paradise Key (D. Fairchild; W. M. Wheeler); no specific locality (J. N. Knull); *Highlands Co.*: Archbold Biol. Stn. (R. Silberglied); Highlands Hammock State Park (L. & C. W. O'Brien); near Sebring (R. W. Klein); no specific locality (F. J. Moore); *Hillsborough Co.*: no specific locality (J. C. Bowyer); *Lake Co.*: no specific locality (W. A. Hiers); *Lee Co.*: Ft. Meyers [= Ft. Myers]; *Monroe Co.*: Lower Matecumbe Key (W. M. Wheeler); N. Key Largo (R. W. Klein); Key West; No Name Key (P. S. Ward); *Osceola Co.*: Lake Alfred (M. H. Muma); *Palm Beach Co.*: Boynton Beach (Wood & Davidson); *Sarasota Co.*: Long Branch Key (A. C. Cole); Sarasota (A. C. Cole); 30 mi SE Sarasota (J. Longino).

BAHAMAS: Andros Island (W. M. Wheeler); Mangrove Cay, Andros Island (B. Cole); Conception Island (G. Greenway); Gun Point, Crooked Island (B. Valentine & R. Hamilton); New Providence (B. Cole).

CUBA: Aguada de Pasajeros (W. M. Wheeler); Anafe, Havana (G. Aguayo); Carnoa, Havana (G. Aguayo); Cayamas (Baker; E. A. Schwartz); Cienaga de Japata (W. M. Wheeler); Guanajay, Pinar del Rio (E. O. Wilson); Guavivo Cave, Soledad (F. Smith); Jiquari (Barbour & Shaw); La Milpa, near Cienfuegos (G. Salt); Pinares Oriente (W. M. Mann); Santa Clara, Las Villas Prov. (E. O. Wilson); Soledad, Cienfuegos (C. T. & B. B. Brues; W. S. Creighton; J. G. Myers; F. Smith; N. A. Weber).

HAITI: Grande Rivière (W. M. Mann); Mtns. N. of Jacmel (W. M. Mann).

JAMAICA: Troy (Wight); Balaclava (Wight).

Pseudomyrmex elongatus Mayr

(Figs. 7, 8, 24, 31)

Pseudomyrma elongata Mayr, 1870, p. 413. Syntype worker(s), Colombia, (Lindig) (not in NHMV) [not examined].

Pseudomyrma elongata var. *tandem* Forel, 1906, p. 228. Syntype workers, El Hiquito, near San Mateo, Costa Rica (P. Biolley) (MNHN) [Examined] [Synonymy by Creighton, 1955, p. 18].

Pseudomyrma elongata Mayr; Wheeler, 1932, p. 4 (partim).

Pseudomyrma elongata Mayr; Creighton, 1950, pp. 79–80 (partim).

Pseudomyrmex elongata Mayr; Creighton, 1955, pp. 17–20 (partim).

Pseudomyrmex elongatus Mayr; Wilson, 1964, p. 4.

Worker Measurements ($n = 24$, except for HL, HW, CI, REL, REL2, and PLI, where $n = 50$): HL 0.78–0.91, HW 0.56–0.64, MFC 0.013–0.024, CI 0.68–0.74, OI 0.52–0.58, REL 0.50–0.58, REL2 0.73–0.82, OOI 0.13–0.48, VI 0.82–0.90, FCI 0.021–0.041, SI 0.42–0.48, SI2 0.55–0.64, FI 0.45–0.56, PDI 0.95–1.45, MPI 0.036–0.072, NI 0.55–0.63, PLI 0.76–0.91, PWI 0.62–0.74, PPWI 1.09–1.40.

Worker Diagnosis.— A small, brown species with elongate head and eyes (HW 0.56–0.64, CI 0.68–0.74); frontal carinae subcontiguous; occipital margin flat or slightly concave, in full-face dorsal view; basal and declivitous faces of propodeum well differentiated; petiole short, broad, and rounded (PLI 0.76–0.91); postpetiole wider than long. Head densely punctate

and usually more or less opaque; remainder of body finely punctate or coriarius-imbricate, varying from opaque to sublucid. Erect pilosity and fine appressed pubescence present on most parts of body, including mesonotum and propodeum; fourth abdominal tergite with a rather dense mat of appressed pubescence.

Comments.— This is the smaller of two *elongatus*-like species in North America. I am considering it conspecific with *P. elongatus* Mayr on the basis of (i) the original description of *P. elongatus*, particularly the indication that HL is 1.5 times HW, and (ii) worker material from Costa Rica (leg. Biolley) (MNHN, NHMV) determined as *P. elongatus* by Mayr and Forel. There is a confusing variety of *elongatus*-like forms in Central and South America, which require detailed taxonomic study. Until such a study is carried out, it seems expedient to refer to the North American species as *P. elongatus* and to leave *P. tandem* Forel as a provisional synonym.

P. subater Wheeler & Mann (1914), originally described as a subspecies of *P. elongatus*, was recognized as a distinct species by Creighton (1955). It may be distinguished from *P. elongatus* and *P. cubaensis* by the shinier integument, conspicuous pilosity (grading insensibly from appressed pubescence to fine suberect and erect setae), broad head (CI 0.83–0.88), short eyes (REL2 0.54–0.58 in *P. subater*, > 0.62 in *P. elongatus* and *P. cubaensis*), distinct petiolar shape (gradually inclined anterior face rounded into a sharply declining posterior face so that NI 0.61–0.72), and conspicuous anteroventral tooth on the postpetiole. Apart from two “cotype” workers in the MCZ from Haiti, I have seen material of *P. subater* (misidentified as *P. elongatus*) from the Bahamas (Andros Island, Nassau) and the same, or a closely related species, from Jamaica (Kingston)). Wheeler’s (1905) record of “*elongatus*” from the Bahamas appears to be based on a combination of *P. subater* and *P. cubaensis*, judging from material in the MCZ.

Recent collections of *P. subater* from the Bahamas by Blaine Cole show that this species has striking bright orange queens, which look superficially like those of *P. pallidus*. Cole also made a collection from a single *Cladium* culm which contained both *P. subater* and *P. cubaensis* workers. These findings suggest that Wheeler’s (1905) and Mann’s (1920) records of dulotic associations between “*flavidula*” and “*elongata*” may have been based in part on pure colonies of *P. subater*, or mixed colonies of *P. subater* and *P. cubaensis*.

Biology.— *P. elongatus* nests in dead twigs in a variety of woody shrubs and trees. I have collected *P. elongatus* colonies in twigs of *Avicennia germinans*, *Baccharis halimifolia*, *Laguncularia racemosa* and *Rhizophora mangle* in Florida, and in *Gliricidia sepium*, *Helicteres*, and *Inga* in Costa Rica and Panama. Among museum material there are records of *P. elongatus* nesting in a “climbing vine” and “mangrove stems” in Florida, in *Quercus virginiana* and *Prosopis* (Texas), and in *Quercus fusiformis* (Nuevo Leon, Mexico).

Material Examined (GCW, LACM, MCZ, PSW, UCD, USNM).—

FLORIDA: *Collier Co.*: Everglade[s] (W. T. Davis); *Dade Co.*: Coconut Grove; Miami; Rattlesnake Hammock, Homestead (R. Gregg); Shark Valley, Everglades Natl. Pk. (P. S. Ward); no specific locality (J. N. Knull); *Highlands Co.*: Archbold Biol. Stn., Lake Placid (T. C. Schneirla); *Lee Co.*: Ft. Myers (W. M. Barrows); *Monroe Co.*: Big Pine Key (E. O. Wilson); John Pennkamp St. Pk., < 5 m (P. S. Ward); Key Largo; Key West (E. O. Wilson); N. Key Largo (R. W. Klein); Plantation Key (E. O. Wilson).

TEXAS: *Cameron Co.*: 5 mi W Boca Chica (G. C. & J. Wheeler); 10 mi W Boca Chica (R. R. Snelling); Harlingen (W. Buren); *Hidalgo Co.*: Mission (W. Buren); Monte Alto (W. S. Creighton); *Kenedy Co.*: 26 mi N Raymondsville (W. S. Creighton).

MEXICO: *Nayarit*: Maria Magdalena, Is. Tres Marias (R. R. Snelling); *Nuevo Leon*: El Pastor, Montemorelos, 2000 ft (W. S. Creighton); *San Luis Potosi*: Rio Amahac, Tamazunchale, 300 ft (W. S. Creighton); 3 mi N. Valles (W. S. Creighton); *Sinaloa*: Mazatlan (P. J. Spangler); *Tamaulipas*: Cañon de el Abra, 1000 ft (W. S. Creighton).

COSTA RICA: *Guanacaste Prov.*: 1 km SW Pto. Coyote, < 5 m (P. S. Ward); *Puntarenas Prov.*: Llorona, Corcovado Natl. Park, 10 m (P. S. Ward); Manuel Antonio Natl. Pk., 5 m (P. S. Ward); Monteverde, 1200 m (P. S. Ward); Sirena,

Penin. Osa, 50 m (J. Longino).

JAMAICA: Ford 1 mi SE Stony Hill (E. A. Chapin).

PANAMA: 2 km W Gamboa, Canal Zone, 30 m (P. S. Ward); 6 km NW Gamboa, Canal Zone, 50 m (P. S. Ward); 6 km NW Gatun Dam, Canal Zone, 75 m (P. S. Ward).

pallidus group

Pseudomyrmex apache Creighton

(Figs. 9, 10, 17)

Pseudomyrmex apache Creighton, 1952, p. 134. Nidoparatype workers, females, males, Brown Canyon, Baboquivari Mtns., Arizona, 4400 ft, 2.ix.1951, in *Quercus oblongifolia* 502 (W. S. Creighton) (LACM, MCZ) [Examined].

Pseudomyrma pallida; Wheeler (nec F. Smith), 1908, p. 420 (partim).

Pseudomyrmex apache Creighton; Creighton, 1954, pp. 9–15 [Distribution].

Pseudomyrmex apache Creighton; Wheeler & Wheeler, 1956, p. 380 [Description of larva].

Pseudomyrmex apache Creighton; Creighton, 1963, pp. 1–4 [Biology].

Pseudomyrmex apache Creighton; Wheeler & Wheeler, 1973, pp. 41–42.

Worker Measurements ($n = 35$): HL 1.02–1.30, HW 0.83–1.04, MFC 0.033–0.066, CI 0.75–0.84, OI 0.58–0.65, REL 0.39–0.44, REL2 0.48–0.54, PPI 1.10–2.00, VI 0.74–0.84, FCI 0.034–0.070, SI 0.46–0.51, SI2 0.90–1.00 FI 0.38–0.44, PDI 0.87–1.19, MPI 0.007–0.044, NI 0.51–0.64, PLI 0.54–0.61, PWI 0.48–0.56, PPWI 1.02–1.19.

Worker Diagnosis.— Head broad; eyes short (EL subequal to SL); anterior clypeal margin laterally rounded; frontal carinae subcontiguous, MFC subequal to the basal width of scape; occipital margin flat to broadly convex, in full-face, dorsal view; pronotum with weak lateral margination; metanotal groove usually weak; petiole relatively short, broad, and high with a rather sharply inclined anterior face. Head opaque to sublucid, densely punctulate on a coriarius background; mesosoma and petiole subopaque, coriarius-imbricate; postpetiole and gaster opaque to sublucid, covered with numerous, fine piligerous punctures. Erect setae sparsely present on scape, head, pronotum, petiole, postpetiole, gaster, and legs (generally absent on mesonotum and propodeum); typically four pairs of erect setae on dorsum of head, and two or three pairs each on pronotum, petiole, and postpetiole. Fine, appressed pubescence scattered over body, including fourth abdominal tergite. Rich orange-brown, the head (and sometimes legs and gaster) a little darker.

Comments.— Although I have placed *P. apache* in the *pallidus* group as a matter of convenience, it is a rather distinct species showing only superficial resemblance to other members of the group. It is the only species to possess such well separated frontal carinae, laterally rounded anterior clypeal margin, short eyes relative to scape length, and (in the male) ventrally pointed pygidium. *P. apache* workers also tend to be larger, more densely sculptured (hence less shiny), and more setose than those of other *pallidus* group species. Size alone (worker HW > 0.83) will separate *P. apache* from all species except *P. pallidus* and *P. seminole*. Apart from character differences outlined in the keys (of which eye size relative to scape length and shape of male terminalia are most distinctive), *P. apache* can usually be distinguished from *P. pallidus* and *P. seminole* by the presence of a pair of erect setae, one on either side of the median ocellus, in the worker. In *P. apache* workers these two setae are always present and usually as long as the ocellar distance (OD). In *P. seminole* and *P. pallidus* workers these setae are either absent or shorter than OD.

Biology.— A denizen of xeric habitats, *P. apache* nests in sizable dead branches (1–12 cm diameter) of various trees (especially live oaks) and large woody shrubs, usually taking advantage of beetle-bored cavities. By state and country, nest-site records are as follows:

Texas: *Prosopis glandulosa*, *Quercus grisea*.

Arizona: *Populus* sp., *Prosopis* sp., *Quercus arizonica*, *Q. emoryi*, *Q. grisea*, *Q. oblongifolia*, *Q. turbinella*.

California: *Arctostaphylos manzanita*, *Fraxinus* gall, *Pinus attenuata* cone, *Quercus chrysolepis*, *Q. wislizenii*, *Umbellularia californica*.

Mexico: *Prosopis* sp., *Quercus emoryi*, *Q. fusiformis*, *Q. oblongifolia*, *Q. santaclarensis*.

Of 13 nests which I have dissected (from Texas, Arizona and California), five contained no dealate females, six contained a single queen, one contained two functional (i.e. inseminated) queens, and one contained 6 dealate queens. Thus this species is at least occasionally polygynous and (judging from the queenless nests) polydomous. For two of the five queenless nests, queenright nests were located on the same tree or shrub.

I have seen two instances of lone foraging (presumably colony founding) dealate queens: one on the trunk of a *Quercus arizonica* tree in September (Arizona) and the other on an *Arctostaphylos* bush in February (northern California). The latter queen was dissected and found to be inseminated but possessing preoviposition ovaries (ovarioles short; corpora lutea absent). Alates of *P. apache* have been collected in March, April, and July to November, suggesting that mating may occur in more than one season.

Material Examined (BMNH, GCW, LACM, MCZ, PSW, UCD, USNM).—

ARIZONA: *Cochise Co.*: Carr Canyon, Huachuca Mtns., 5400 ft (W. S. Creighton), 6200 ft (C. W. O'Brien); Cave Crk. Ranch, Chiricahua Mtns., 5000 ft (G. E. Wallace); Chiricahua Mt. (D. J. and J. N. Knull); Chiricahua Mtns. (J. N. Knull); Chiricahua Natl. Monum. Cprgd., 5400 ft (W. S. Creighton); Cochise Stronghold, Dragoon Mtns., 5200 ft (W. S. Creighton); Coronado Peak, 2020 m (P. S. Ward); Garden Canyon, Huachuca Mtns., 5800 ft (W. S. Creighton); Huachuca Mt. (J. N. Knull); Miller Canyon, Huachuca Mtns. (W. S. Creighton); Portal (G. Alpert); 3 km SW Portal, 1510 m (P. S. Ward); 7 km SE Sunnyside, 1670 m (P. S. Ward); *Gila Co.*: Globe (Nuttig); *Graham Co.*: Cottonwood Canyon, Peloncillo Mtns., 4800 ft (W. S. Creighton); *Graham Mtns.*, 3500-4500 ft (R. M. Bohart); Post Canyon, Pinaleno Mtns., 5000-6000 ft (W. M. Wheeler); *Mohave Co.*: Hualapai Mtns., S. of Kingman, 1450 m (E. Schlinger); *Pima Co.*: Abra Wash, Growler Mtns., Organpipe Cactus Natl. Monum., 1300 ft (W. S. Creighton); Alamo Canyon, Ajo Mtns., Organpipe Cactus Natl. Monum., 2200 ft (W. S. Creighton); Brown Canyon, Baboquivari Mtns., 4400 ft (W. S. Creighton); Forestry Cabin, Baboquivari Mtns., 3500 ft (W. S. Creighton); Organpipe Cactus Natl. Monum. (E. R. Tinkham); Sabino Canyon (V. L. Vesterby); San Miguel (E. D. Alpert); Tucson (J. Knull); *Santa Cruz Co.*: Canelo Pass, 5300 ft (W. S. Creighton); Madera Canyon, Santa Rita Mtns. (W. S. Creighton), 4880 ft (C. R. Kovacic; V. L. Vesterby); Nogales (Burdine; D. J. & J. N. Knull); Peña Blanca Springs, 3700 ft (W. S. Creighton); Sweetwater, Santa Rita Mtns., 4000 ft and 6000 ft (W. S. Creighton); Tumacacori Mt. (D. J. & J. N. Knull); *county unknown*: Catal Springs (Hubbard & Schwartz); Santa Catalina Mtns. (M. Chrisman); Santa Rita Mtns. (R. M. Bohart; J. Knull).

CALIFORNIA: *Butte Co.*: 6 km N Feather Falls, 600 m (P. S. Ward); *Colusa Co.*: 1 km W Fout Springs, 600 m (P. S. Ward); *Imperial Co.*: Winterhaven (R. L. Westcott); *Lake Co.*: Borax Lake (E. L. Westcott); *Los Angeles Co.*: Altadena; Eaton Canyon Pk. (M. E. Thompson); Foothill, Pasadena (A. H. Sturtevant); 3 mi N. Mt. Baldy (E. Weidert); Tanbark Flat (R. C. Bechtell; R. M. Bohart); *Napa Co.*: Mt. St. Helena (J. S. Buckett); 4 km E summit Mt. St. Helena, 450 m (P. S. Ward); *Orange Co.*: Irvine Pk. (K. Brown); Trabuco Canyon (M. E. Irwin); Trabuco east (E. Eidert); *Riverside Co.*: Blythe (R. M. Hardman); Deep Canyon (W. P. MacKay); Dripping Springs, Agua Tibia Mtns., 1500 ft (W. S. Creighton); Pinon Flat, San Jacinto Mtns. (R. L. Macdonald); Poppet Flats (G. Clark); Riverside (E. I. Schlinger); Whitewater (A. L. Melander); Winchester (W. Icenogle); *San Bernardino Co.*: nr. Cajon pass; *San Diego Co.*: Jacumba (D. J. & J. N. Knull); 5.9 mi NE Ramona, Hwy. 78 (S. & S. Fromer, S. Larisch); 5.2 mi NW Ramona, Hwy. 78 (S. & S. Fromer, S. Larisch); no specific locality; *Santa Barbara Co.*: Canyon del Medio, Santa Cruz I. (R. O. Schuster & E. C. Toftner); *Santa Clara Co.*: no specific locality; *Solano Co.*: Cold Canyon, 420 m (P. S. Ward); *Tehama Co.*: 26 km WSW Red Bluff, 240 m (P. S. Ward); *Tulare Co.*: Ash Mtn. Powerhouse #3 (D. J. Burdick; J. A. Halstead); Ash Mtn., Sequoia Natl. Pk. (M. G. Fitton); Horse Creek Rd. (O. L. Brawner); *Ventura Co.*: Saticoy (R. E. Barrett); *Yolo Co.*: 3 km SW Guinda, 150 m (P. S. Ward); 4 km NW Rumsey, 150 m (P. S. Ward); *county unknown*: mtns. near Claremont [Los Angeles or San Bernardino Co.] (Baker).

DISTRICT OF COLUMBIA: Washington (B. P. Currie) [Dubious locality record].

TEXAS: *Bexar Co.*: San Antonio (P. S. Ward); *Duval Co.*: Freer (R. R. Rodgers); San Diego; *Edwards Co.*: Camp Wood (C. R. Ward); *Goliad Co.*: no specific locality (J. D. Mitchell); *Hidalgo Co.*: Monte Alto, 60 ft (W. S. Creighton); *La Salle Co.*: Fowlerton, 300 ft (W. S. Creighton); *Maverick Co.*(?): El Indigo [= El Indio?] (D. H. Bixby); *Presidio Co.*: Arsaca Canyon, Chinati Mtns., 4800 ft (W. S. Creighton); *Starr Co.*: no specific locality (D. J. & J. N. Knull); *Travis Co.*: Austin (P. S. Ward); *Uvalde Co.*: no specific locality (D. J. & J. N. Knull).

MEXICO: *Baja California Norte*: 25 mi N El Arco (W. H. Ewart); *Baja California Sur*: 72 mi NW La Paz, 100 ft (R. R. Snelling); San José del Cabo; 7 mi NW Santa Rosalia, 850 ft (R. R. Snelling); 2.7 mi SE Valle Peridido; *Chihuahua*: 3 mi S Encinillas, 4900 ft (W. S. Creighton); 16 mi W Gral. Trias, 5800 ft (W. S. Creighton); Nogales Ranch, Sierra de en Medio, 5200 ft (W. S. Creighton); Ojo del Cerro Chilicote (C. H. T. Townsend); 23 mi S Parral, 5500 ft (W. S. Creighton); 34 mi S Parral, 5800 ft (W. S. Creighton); *Durango*: Villa Ocampo [=Ocampo], 5700 ft (W. S. Creighton); *Nuevo Leon*: China, 600 ft (W. S. Creighton); *Sonora*: 30 mi SE Agua Prieta (V. Roth); 4.8 mi S Cananea (V. Roth).

Pseudomyrmex brunneus F. Smith

(Figs. 13, 15)

Pseudomyrma brunnea F. Smith (1877), p. 63. Holotype (unique syntype) worker, Mexico (BMNH) [Examined].

Pseudomyrma brunnea var. *nigrita* Enzmann, 1945, p. 82. Syntype workers, Mirador, Mexico (E. Skwarra) (MCZ) [Examined]. *Syn. nov.*

Worker Measurements ($n = 10$): HL 0.77–0.86, HW 0.67–0.72, MFC 0.012–0.024, CI 0.83–0.90, OI 0.57–0.63, REL 0.51–0.56, REL2 0.58–0.64, OOI 0.67–1.20, VI 0.70–0.78, FCI 0.017–0.035, SI 0.43–0.50, SI2 0.69–0.80, FI 0.41–0.45, PDI 0.56–0.75, MPI 0.052–0.075, NI 0.57–0.65, PLI 0.47–0.58, PWI 0.54–0.65, PPWI 1.26–1.54.

Worker Diagnosis.— Small, brown species, with wide head and broadly rounded occipital margin (HW 0.67–0.72, CI 0.83–0.90). Similar to *P. ejectus* F. Smith (*q.v.*) except as follows: basal face of propodeum between one half and three quarters the length of declivitous face (PDI 0.56–0.75); petiole shorter and broader than that of *P. ejectus* (PWI 0.54–0.65); petiolar node somewhat displaced posteriorly; postpetiole short and wide (PPWI 1.26–1.54). Front of head opaque, densely coriarius-imbricate; sculpture becoming weaker towards the vertex, with scattered, fine punctures on a (usually) sublucid, coriarius background; mesosoma subopaque, coriarius to coriarius-imbricate; petiole, postpetiole, and gaster increasingly (in that order) less coriarius and more smooth and shining. Erect pilosity very sparse; appressed pubescence scattered over body; abdominal tergite IV with appressed hairs separated by about their lengths, and not obscuring the shiny integument. Body dark brown, little or no contrast in color between the head, mesosoma, petiole, postpetiole, or gaster; mandibles and apical ends of tarsi luteous.

Comments.— This appears to be an uncommon Mexican species, which occurs sympatrically with *P. ejectus*. The major differences between the two species are in the shapes of the propodeum, petiole, and postpetiole (note especially the non-overlapping values of PWI and PPWI). In addition, *P. brunneus* tends to have a more densely sculptured (and opaque) head than *P. ejectus* and to exhibit less contrasting light and dark brown coloration on the mesosoma, petiole and postpetiole.

Biology.— At Cola de Caballo, near Monterrey, I collected workers and larvae of *P. brunneus* in dead twigs of a small tree, probably *Melia azedarach*, and in the dead stalk of an unidentified mint. The latter nest contained a single dealate queen. *P. ejectus* was also found nesting in a dead mint stalk at this locality.

Material Examined (BMNH, MCZ, PSW, UCD).—

MEXICO: *Nuevo Leon*: Cola de Caballo, 38 km SSE Monterrey, 600 m (P. S. Ward); *Veracruz*: Mirador (E. Skwarra); *state unknown*: "Mexico."

Pseudomyrmex ejectus F. Smith

(Figs. 14, 16, 23, 30)

Pseudomyrma ejecta F. Smith (1858), p. 157. Two syntype workers, "Brazil?" (BMNH) [Examined]. One syntype here designated as LECTOTYPE.

Pseudomyrma brunnea; Wheeler (nec F. Smith), 1908, pp. 420–421.

Pseudomyrma brunnea; Mitchell & Pierce (nec F. Smith), 1912, p. 69.

Pseudomyrma brunnea; Wheeler (nec F. Smith), 1913b, p. 240.

Pseudomyrma brunnea; Wheeler (nec F. Smith), 1932, p. 3.

Pseudomyrma brunnea; Creighton (nec F. Smith), 1950, p. 79.

Pseudomyrmex brunneus; Wheeler & Wheeler (nec F. Smith), 1956, p. 382 [Description of larva].

Worker Measurements ($n = 50$): HL 0.65–0.97, HW 0.56–0.81, MFC 0.007–0.021, CI 0.78–0.89, OI 0.52–0.62, REL 0.51–0.59, REL2 0.61–0.70, OOI 0.46–1.52, VI 0.64–0.78, FCI 0.010–0.030, SI 0.43–0.49, SI2 0.64–0.76, FI 0.36–0.50, PDI 0.70–1.07, MPI 0.046–0.097, NI 0.48–0.60, PLI 0.43–0.57, PWI 0.40–0.52, PPWI 0.93–1.25.

Worker Diagnosis.— Head wide, broadly rounded (HW 0.56–0.81, CI 0.78–0.89); anterior clypeal margin medially straight, laterally angulate; frontal carinae closely contiguous; occipital margin convex, flat, or slightly concave, in full face, dorsal view; pronotum broadly rounded; metanotal groove wide and rather deep (MPI 0.046–0.097); basal face of propodeum subequal in length to declivitous face, and poorly differentiated from it (PDI 0.70–1.07); petiole and postpetiole relatively long and slender (PWI 0.40–0.52); anteroventral tooth present on petiole. Head subopaque to weakly shining, the frons punctulate on a coriarius imbricate background; sculpture weakening towards the vertex, which is correspondingly more shiny; mesosoma and petiole sublucid, coriarius-imbricate; postpetiole and gaster more or less smooth and shining. Erect pilosity very sparse; appressed pubescence inconspicuous; appressed hairs on abdominal tergite IV not forming a dense mat nor obscuring the shiny integument. Head (except clypeus and mandibles), mesonotum, propodeum, and gaster dark brown; pronotum, petiole, and postpetiole generally a lighter brown, of varying contrast; clypeus, mandibles, and apices of legs light brown to pale luteous.

Comments.— The lectotype and paralectotype workers of *P. ejectus* in the BMNH agree well with the common species in southeastern United States which has been masquerading under the name “*brunneus*”. I have also seen material which I would consider conspecific with *P. ejectus* from Mexico, Jamaica, Belize, and Costa Rica, but not from South America. (There are other *ejectus*-like taxa in Central and South America, some undescribed.) It seems likely that the types of *ejectus* came from the United States or Central America rather than Brazil. Differences between *P. ejectus* and *P. brunneus* are discussed under the latter species.

Described as a variety *P. ejectus*, *P. peruvianus* Wheeler (1925, p. 11) is here considered to be a distinct species (*stat. nov.*). Three syntype workers in the MCZ from Chaquimayo, Peru (leg. Holmgren) have a smooth, shining, punctulate head whose light brown color contrasts with the dark brown gaster; more clearly differentiated basal and declivitous faces of the propodeum than *P. ejectus* (PDI 1.06–1.09); and a short, high, and (in dorsal view) thin petiole such that PLI 0.60–0.65 and PHI 0.77–0.83 (PLI 0.43–0.57 and PHI 0.54–0.78 in *P. ejectus*).

Biology.— *P. ejectus* nests in dead twigs or stalks of woody and herbaceous plants. Among the *P. ejectus* nest series which I have examined there are records from the following plant genera: *Carya*, *Cladium*, *Conostegia*, *Prosopis*, *Quercus*, *Rhus*, *Spilanthes*, *Vernonia*, and *Vitis*. In southeastern United States alates have been collected in the months of March, June, July, and September. Three out of five nests which I dissected (from Florida, Texas, and Mexico) contained a single dealate female; the other two nests were queenless. In Florida some nests of this species are polygynous (R. W. Klein, pers. comm.).

Material Examined (BMNH, GCW, LACM, MCSN, MCZ, NHMB, PSW, UCD, USNM).—

ALABAMA: Baldwin Co.: Jackson's Oak (W. S. Creighton); Marlow's Ferry, Fish R. (W. S. Creighton); Mobile Co.: Dog R., Mobile (W. S. Creighton); Irvington (Van Aller); Mobile (W. D. Pierce); Theodore (A. H. Sturtevant); Whistler (A. H. Sturtevant); county unknown: Kushla (A. H. Sturtevant).

FLORIDA: *Alachua Co.*: Gainesville (R. W. Klein; N. L. H. Krauss); *Collier Co.*: Everglades (W. M. Barrows), Immokalee (M. Deyrup); Royal Palm Pk. (Melander). *Dade Co.*: Coconut Grove; Homestead (W. F. Buren; G. B. Merrill); Homestead Air Force Base (G. C. & J. Wheeler); Long Pine Key (W. M. Wheeler); Miami (W. T. Davis); Old Flamingo Rd., Everglades Natl. Pk. 10 m (P. S. Ward); Paradise Key (W. M. Wheeler); Pinelands Trail, Everglades Natl. Pk. (G. C. and J. Wheeler); Shark Valley, Everglades Natl. Pk. (P. S. Ward); Visitor Centre, Everglades Natl. Pk. (G. C. & J. Wheeler); no specific locality (J. N. Knull); *Duval Co.*: Fort George; *Highlands Co.*: Archbold Biol. Stn., Lake Placid (T. C. Schneirla, J. Walker); Highlands Hammock St. Pk. (P. S. Ward); Sebring (I. E. Harper); *Hillsborough Co.*: Pine Crest [=Pinecrest] (W. M. Wheeler); no specific locality (J. C. Bowyer); *Indian River Co.*: Vero Beach (L. & C. W. O'Brien); *Leon Co.*: Anders Branch, Tall Timbers Res. Stn. (J. F. Lynch); Tallahassee (G. C. & J. Wheeler); *Monroe Co.*: Key Largo (H. V. Weems); 12 mi N Key Largo (P. S. Ward); N. Key Largo (R. W. Klein); *Orange Co.*: no specific locality (C. Nelson; B. L. Smith; E. Storrs); *Palm Beach Co.*: Boynton Beach (Wood & Davidson); Palm Beach; *Pinellas Co.*: Belle Air [= Belleair]; Dunedin (Blatchley); Largo (Bradley & Knorr); *Taylor Co.*: Williams Landing (R. Smith); *Volusia Co.*: Haw Creek (T. Pergande?), county unknown: Everglades Natl. Pk. (G. C. & J. Wheeler).

GEORGIA: *Chatham Co.*: Savannah (H. T. Vanderford); *Decatur Co.*: no specific locality (Kannowski); *Glynn Co.*: Brunswick (N. L. H. Krauss); *Seminole Co.*: no specific locality (Kannowski).

LOUISIANA: *Beauregard Co.*: DeRidder (W. Buren).

MARYLAND: *St. Marys Co.*: Leonardtown (O. L. Cartwright).

SOUTH CAROLINA: *Chesterfield Co.*: Cheraw St. Pk. (G. C. & J. Wheeler).

TEXAS: *Bexar Co.*: Ft. S. Houston (R. B. Kimsey); San Antonio (P. S. Ward; R. Williams); San Antonio NE Preserve (R. B. Kimsey); *Brazoria Co.*: 4 mi SW West Columbia (P. S. Ward); *Cameron Co.*: 10 mi W Boca Chica (W. S. Creighton); Brownsville (P. J. Darlington; J. Knull); *Comal Co.*: New Braunfels (W. M. Wheeler); *Hidalgo Co.*: Bentsen R. Grande St. Pk., Mission (W. S. Creighton; P. S. Ward); Santa Ana Refuge (P. S. Ward); no specific locality (J. Knull); *Kenedy Co.*: 26 mi N Raymondsville (W. S. Creighton); *Live Oak Co.*: Three Rivers (W. S. Creighton); *McLennan Co.*: Waco; *Travis Co.*: Austin (G. Bush & W. L. Brown; P. S. Ward); *Victoria Co.*: Victoria (W. E. Hinds; J. D. Mitchell).

MEXICO: *Guerrero*: 18 mi S Chilpancingo (F. D. Parker & L. A. Stange); *Nuevo Leon*: Cola de Caballo, 38 km SSE Monterrey, 600 m (P. S. Ward); *Quintana Roo*: San Miguel, Cozumel I. (N. L. H. Krauss); *Tabasco*: Frontera (R. Andrews); *Tamaulipas*: Matamoros (F. F. Bibby); *Veracruz*: Los Tuxtlas (R. L. Jeanne); Mirador (E. Skwarra); Palma Sola (R. Andrews); Remutadero (E. Skwarra); Tinajas (F. D. Parker & L. A. Stange).

BELIZE: Rideau Camp (P. Broomfield).

COSTA RICA: *Guanacaste Prov.*: Agua Caliente (W. M. Wheeler); *Puntarenas Prov.*: Monteverde, 1200 m (P. S. Ward); *San José Prov.*: Alfombra, 850 m (P. S. Ward); San José (W. M. Wheeler).

JAMAICA: Lapland, Catadupa; Ford 1 mi SE Stony Hill (E. A. Chapin).

Pseudomyrmex leptosus Ward sp. nov.

(Figs. 19, 26, 34, 35, 38)

Holotype queen.—Payne's Prairie, 8 mi S Gainesville, Alachua Co., Florida, 5.viii.1982, R. W. Klein (MCZ) (ex lab colony established from a mixed nest of *P. leptosus* and *P. ejectus* originally collected 16.v.1982). HW 0.70, HL 0.86, EL 0.41, PL 0.53, PH 0.27.

Paratype queens, males.—Payne's Prairie, 8 mi S Gainesville, R.W. Klein (ex lab colony established from mixed nest of *P. leptosus* and *P. ejectus* originally collected 16.v.1982); Gainesville, Alachua Co., Florida, R. W. Klein (ex lab colony established from mixed nest of *P. leptosus* and *P. ejectus* originally collected 15.v.1982) (BMNH, LACM, MCZ, PSW, UCD, USNM).

Worker.—Unknown.

Queen Measurements ($n = 11$): HL 0.83–0.91, HW 0.67–0.70, MFC 0.019–0.027, CI 0.77–0.82, OI 0.53–0.59, REL 0.47–0.51, REL2 0.59–0.63, OOI 0.92–1.58, VI 0.68–0.75, FCI 0.028–0.039, CDI 0.047–0.057, SI 0.45–0.48, SI2 0.75–0.77, FI 0.42–0.47, NI 0.60–0.68, PLI 0.47–0.51, PLI2 0.72–0.84, PHI 0.59–0.68, PWI 0.43–0.51, PWI2 0.50–0.57, PPWI 1.02–1.18, PPWI2 0.61–0.67.

Queen Diagnosis.—A small orange species with broadly rounded, shiny head (HW 0.67–0.70, VI 0.68–0.75); anterior clypeal margin medially straight or slightly convex, laterally angulate; distance between frontal carinae less than basal width of scape; occipital margin convex, flat, or weakly concave, in full-face, dorsal view; lateral margins of pronotum rounded; basal face of propodeum rounding into declivitous face; petiole relatively slender, twice as long as high; anterior face of petiole convex, in lateral view; postpetiole as wide or wider than long. Front of head finely but densely punctulate, on a more or less smooth, shining background; fine

punctures becoming less dense towards the occiput, which is also smooth and shining; petiole and most of mesosoma sublucid, finely or obscurely punctulate on a weak coriarius background; propleuron subopaque, coriarius-imbricate; postpetiole and gaster weakly shining, the sheen partially obscured by numerous, fine piligerous punctures. Erect pilosity very sparse; several erect setae on dorsum of head, pronotum, mesonotum, metanotum, petiole, postpetiole and gaster; erect pilosity essentially absent from propodeum, scapes, and mid and hind femora. Fine appressed pubescence present, but not obscuring sculpture on most parts of body; appressed pubescence moderately dense on abdominal tergite IV, only partially obscuring the shiny integument. Body light orange-brown; a conspicuous pair of anterolateral, dark fuscous patches on abdominal tergite IV.

Comments.— This species is known only from queens and males collected in, or reared from, two mixed nests of *P. leptosus* and *P. ejectus* from the vicinity of Gainesville, Florida (R. W. Klein, leg.).³ The original colonies each contained two dealate queens of *P. leptosus* (together with *P. ejectus* workers, and brood of both species), and Klein subsequently reared *P. leptosus* alates in the laboratory.

P. leptosus queens are readily distinguishable from those of *P. apache* and *P. seminole* on the basis of size alone ($HL > 1.25$ in *P. apache* and *P. seminole*, $HL < 0.95$ in *P. leptosus*). *P. leptosus* queens differ from those of *P. simplex* by the possession of a wider, more broadly rounded head ($CI \geq 0.77$, $VI \leq 0.75$, in *P. leptosus*; $CI \leq 0.77$, $VI \geq 0.80$, in *P. simplex*), shorter eyes ($REL2 \leq 0.63$ in *P. leptosus*; $REL2 \geq 0.65$ in *P. simplex*), more divergent frontal carinae, and narrower forefemur ($FI\ 0.42-0.47$ in *P. leptosus*, $FI\ 0.49-0.55$ in *P. simplex*). The differences between *P. leptosus* and *P. pallidus* queens are more subtle. All of their measurements and indices overlap, although *P. leptosus* tends to be smaller and (more importantly) to possess a more broadly rounded head, so that $VI\ 0.68-0.75$ ($VI\ 0.71-0.88$ in *P. pallidus*). The most important distinction between the two species lies in the sculpture of the frons and vertex: finely punctate on a predominantly smooth, shiny background in *P. leptosus*; more coarsely punctate on a sublucid, coriarius background in *P. pallidus* (Figures 38, 39). Despite some size-related sculptural variation in *P. pallidus* even the smallest *P. pallidus* queens possess more strongly developed coriarius sculpture on the head than *P. leptosus* queens. The postpetiole and gaster of *P. leptosus* also tend to be shinier than those of *P. pallidus*. There are slight differences in the male genitalia of the two species, as outlined in the key to males.

Biology.— This species is apparently a workerless, social parasite of *P. ejectus*. Details on the life history and behavior of *P. leptosus* will appear elsewhere (R. W. Klein, in prep.).

Material Examined (BMNH, LACM, MCZ, PSW, UCD, USNM).—

FLORIDA: Alachua Co.: Gainesville (R. W. Klein); Payne's Prairie, 8 mi S Gainesville (R. W. Klein).

Pseudomyrmex pallidus F. Smith

(Figs. 20, 27, 36, 37, 39, 42, 43)

Pseudomyrma pallida F. Smith (1855), p. 160. One syntype queen (dealate), one syntype worker, "U.S." (BMNH) [Examined]. Syntype worker here designated as LECTOTYPE.

Pseudomyrma flavidula; Wheeler (nec F. Smith), 1905, pp. 83-85, 87 (partim)

Pseudomyrma flavidula; Wheeler (nec F. Smith), 1908, p. 419.

³I recently received an additional collection of *P. leptosus*, from Munroe Co., Florida (Hwy. 94, 10 mi. W Tamiami Ranger Station, 26.xi.1984, *P. leptosus* queens in nest with *P. ejectus* workers, Blaine Cole leg.).

Pseudomyrma pallida F. Smith; Wheeler, 1908, pp. 419-420 (partim).

Pseudomyrma flavidula; Mitchell & Pierce (nec F. Smith), 1912, p. 69.

Pseudomyrma pallida F. Smith; Mitchell & Pierce, 1912, p. 69.

Pseudomyrma flavidula; Mann (nec F. Smith) 1920, p. 405 (partim).

Pseudomyrma flavidula; Wheeler & Bailey (nec F. Smith), 1920, pp. 260, 265 [Description of larva, and contents of food pellets].

Pseudomyrma flavidula var. *delicatula*; Wheeler & Bailey (nec Forel), 1920, p. 265 (partim) [Description of food pellet contents].

Pseudomyrma flavidula; Wheeler (nec F. Smith), 1932, p. 4 (partim).

Pseudomyrma pallida F. Smith; Wheeler, 1932, p. 4 (partim).

Pseudomyrma pallida F. Smith; Creighton, 1950, pp. 80-82 (partim).

Pseudomyrmex pallidus F. Smith; Wilson, 1964, pp. 4-5 (partim).

Pseudomyrmex pallidus F. Smith; Wheeler & Wheeler, 1973, pp. 41-44.

Worker Measurements ($n = 70$): HL 0.78-1.06, HW 0.68-0.89, MFC 0.011-0.024, CI 0.77-0.91, OI 0.54-0.62, REL 0.45-0.54, REL2 0.53-0.65, OOI 0.78-2.08, VI 0.67-0.84, FCI 0.015-0.033, SI 0.41-0.49, SI2 0.68-0.85, FI 0.37-0.45, PDI 1.10-1.52, MPI 0.022-0.054, NI 0.54-0.67, PLI 0.47-0.62, PWI 0.38-0.52, PPWI 0.85-1.18.

Worker Diagnosis.— Medium-sized species (for the *pallidus* group), with moderately broad head (HW 0.68-0.89, CI 0.77-0.91); anterior clypeal margin medially flat, laterally angulate; distance between frontal carinae less than basal width of scape; eyes moderately long, EL greater than scape length; occipital margin convex, flat or weakly concave, in full-face, dorsal view; lateral margins of pronotum rounded; metanotal groove present but shallow; basal face of propodeum longer than declivitous face, and more or less differentiated from it; petiole slender, with a distinct anterior peduncle and anteroventral tooth. Head subopaque to weakly shining; frons densely punctulate on a coriarius background; punctures less dense on the vertex which remains (at least weakly) coriarius; dorsum of mesosoma and petiole sublucid, coriarius-punctulate, becoming coriarius-imbricate laterally; postpetiole and gaster weakly shining, covered with numerous, very fine piligerous punctures. Erect pilosity sparse, lacking on mesonotum, propodeum, and mid and hind femora; one to several erect setae on dorsum of head, pronotum, petiole, postpetiole, and abdominal tergite IV. Fine, appressed pubescence present on most parts of body, forming a moderately dense mat on abdominal tergite IV, which partially obscures the sheen of the integument. Body orange-brown, with paler mandibles and appendages; a pair of anterolateral fuscous patches sometimes present on abdominal tergite IV.

Comments.— This is the most common and widespread member of the *pallidus* group. *P. pallidus* shows considerable geographical variation in size, sculpture, and body proportions (note wide ranges of some metrics). However the workers are consistently orange-brown in color, with contiguous frontal carinae ($MFC < 0.025$), moderately long eyes ($REL2 > 0.52$), and (at least weakly) coriarius-punctulate sculpture on the vertex. No other Nearctic species possesses this combination of characters. Specific differences between *P. pallidus* and other orange *Pseudomyrmex* (*P. apache*, *P. leptosus*, *P. seminole*, and *P. simplex*) are discussed under those species.

Biology.— *P. pallidus* exhibits diversity in its choice of nesting sites. While it shows a preference for dead stalks or culms of herbaceous plants, it will also nest in dead twigs or branches of shrubs and trees in some localities.

By state, the Nearctic nest-site records are from the following plants (based on personal observations or on museum material which I have examined):

Florida: *Ambrosia artemisiifolia*, *Andropogon*, *Bidens*, *Cladium jamaicense*, *Viola paniculata*.

Georgia: *Callicarba*.

Texas: *Baccharis*, *Heterotheca subaxillaris*, *Iva ciliata*, *Melia azedarach*, *Prunus*, *Ptelea trifoliata*, *Viola paniculata*.

Arizona: *Gossypium thurberi*, *Quercus emoryi*, *Q. oblongifolia*.

California: *Acacia greggii*, *Hyptis emoryi*.

The number of functional queens in a colony varies widely. The majority of *P. pallidus* nests which I dissected from Texas and Florida were queenless or monogynous, but sometimes larger numbers of mated, dealate queens cohabited (up to a maximum of 22). Since *P. pallidus* colonies are often polydomous, the number of queens per colony may be higher.

P. pallidus alates have been collected in every month of the year, indicating that mating occurs in more than one season.

Material Examined (BMNH, GCW, LACM, MCSN, MCZ, MHN, NHMB, PSW, UCD, USNM).—

ALABAMA: *Mobile Co.*: Mobile (Van Aller); Spring Hill, Mobile (W. S. Creighton); Theodore (A. H. Sturtevant); Whistler (A. H. Sturtevant); *county unknown*: Kushla (A. H. Sturtevant)

ARIZONA: *Cochise Co.*: Carr Canyon, Huachuca Mtns., 5400 ft (W. S. Creighton); Huachuca Mtns., T.24S, R.20E, sec. 4, SW quadr., 5850-5900 ft (R. R. Snelling); Portal, Chiricahua Mtns. (R. M. Bohart); Ramsey Canyon, Huachuca Mtns., (W. S. Creighton); *Graham Co.*: Cottonwood Pass, Peloncillo Mtns., 4800 ft (W. S. Creighton) *Maricopa Co.*: Tempe (W. M. Wheeler); *Pima Co.*: Brown Canyon, Baboquivari Mtns., 4400 ft (W. S. Creighton); Forestry Cabin, Baboquivari Mtns., 3500 ft (W. S. Creighton); Molino Basin, Santa Catalina Mtns., 4200 ft (W. S. Creighton); *Santa Cruz Co.*: Bathtub Canyon, Santa Rita Mtns. (L. F. Byars); Nogales (C. A. Geesey; C. H. Spitzer); *county unknown*: Santa Rita Mtns., (J. Knull).

CALIFORNIA: *Riverside Co.*: Deep Canyon (G. C. & J. Wheeler); *San Bernardino Co.*: 49 Palms, Joshua Tree Natl. Monum., 900 m (P. S. Ward); Yucca Valley (Melander).

FLORIDA: *Alachua Co.*: Gainesville (C. J. Drake; R. W. Klein); Payne's Prairie, 8 mi S Gainesville (R. W. Klein); *Collier Co.*: Marco (W. T. Davis); *Dade Co.*: Agri. Res. Educ. Centre, Homestead (R. W. Klein); Dodge I., Miami (G. Stegmaier); Homestead (C. W. O'Brien); Homestead Air Force Base (G. C. & J. Wheeler); Old Flamingo Rd., Everglades Natl. Pk., 10 m (P. S. Ward); Miami Beach (W. Wirth); no specific locality (J. Knull); *Duval Co.*: Fort George; *Glades Co.*: Fisheating Creek, Palmdale (M. Deyrup); *Highlands Co.*: Archbold Biol. Stn., Lake Placid (T. C. Schneirla); Highlands Hammock St. Pk. (C. W. O'Brien); *Leon Co.*: Sheep I., Tall Timbers Res. Stn. (J. F. Lynch); *Monroe Co.*: Bahia Honda Recr. Area, 5m (P. S. Ward); Big Pine Key (P. S. Ward; E. O. Wilson); John Pennekamp St. Pk., < 5m (P. S. Ward); 12 mi N Key Largo (P. S. Ward); 16 mi N Key Largo (P. S. Ward); Key West (T. Pergande); Loggerhead Key, 1.9 mi S Cudjoe Key (R. Thorington, J. Layne & P. Cone); Lower Matecumbe Key (W. M. Wheeler); Mrazek Pond, Everglades Natl. Pk. (L. & C. W. O'Brien); No Name Key (P. S. Ward); Refuge Nature Trail, Big Pine Key, 10 m (P. S. Ward); *Pinellas Co.*: Dunedin (Blatchley); *Sarasota Co.*: Long Branch Key, Sarasota (A. C. Cole); *county unknown*: "Florida" (T. Pergande; S. Henshaw).

GEORGIA: *Chatham Co.*: nr. Savannah (R. A. Cushman); *Richmond Co.*: Augusta (R. R. Snelling).

LOUISIANA: *Beauregard Co.*: DeRidder (W. Buren); *Caddo Co.*: Shreveport (W. Buren; R. A. Cushman); *Madison Co.*: Tallulah (E. R. Kalmbach).

MISSISSIPPI: *Adams Co.*: Sibley (A. Fleming); *Jackson Co.*: Pascagoula; *Lauderdale Co.*: Meridian (H. T. Vanderford); *Smith Co.*: Taylorsville (W. S. Creighton)

NEW JERSEY: *Cape May Co.*: Dias Creek.

NORTH CAROLINA: *New Hanover Co.*: Wrightsville [= Wrightsville Beach?] (W. T. Davis).

TEXAS: *Bexar Co.*: San Antonio (G. A. Prucia; P. S. Ward); 10 mi NW San Antonio (W. S. Ross); *Brazos Co.*: College Station (R. S. Peigler); *Cameron Co.*: Brownsville (J. Knull); *Comal Co.*: New Braunfels (Darlington); *Fort Bend Co.*: Richmond (Cushman & Pierce); *Goliad Co.*: no specific locality (J. D. Mitchell); *Gonzales Co.*: Palmetto St. Pk. (P. S. Ward); *Hidalgo Co.*: Bentsen Rio Grande St. Pk. (P. S. Ward); Santa Ana Refuge (P. S. Ward); no specific locality (D. J. & J. N. Knull); *Kleberg Co.*: Padre I. Natl. Seashore (P. S. Ward); *Matagorda Co.*: Wadsworth (P. S. Ward); *Nueces Co.*: Mustang I. St. Pk. (P. S. Ward); Port Aransas, 5 m (P. S. Ward); 3.4 km SW Port Aransas, 5 m (P. S. Ward); 11 km SW Port Aransas, 5 m (P. S. Ward); 18 km SW Port Aransas, 5 m (P. S. Ward); *Travis Co.*: Austin (D. Tupa; W. M. Wheeler); Barton Creek, Austin (P. S. Ward); Brackenridge Field Stn., Austin (P. S. Ward); *Victoria Co.*: Victoria (J. D. Mitchell); *Willacy Co.*: 7 mi N. Rio Hondo (W. S. Creighton); *county unknown*: Devils River (E. A. Schwartz).

MEXICO: *Baja California Sur*: Las Barrancas (W. M. Mann); 7 mi N. Santiago (W. H. Ewart); 2.7 mi SE Valle Perdido (R. R. Snelling); *Chiapas*: Tonola (A. Petrunkewitch); Tuxtla Gutierrez (N. L. H. Krauss); *Chihuahua*: El Paso, Texas, POE (V. J. Shiner); *Durango*: 6 mi E San Lucas, 6200 ft (W. S. Creighton); *Guerrero*: Acapulco (Baker); 18 mi S Chilpancingo (F. D. Parker & L. A. Stange); Revolcadero, nr. Acapulco (N. L. H. Krauss); *Hidalgo*: San Miguel (W. M. Mann); *Morelos*: Cuernavaca (N. L. H. Krauss); *Nayarit*: Tepic; *Nuevo Leon*: Iturbide, 1800 m (P. S. Ward); *Quintana Roo*: San Miguel, Cozumel I. (N. L. H. Krauss); *Sinaloa*: 1.1 mi W El Quelite (M. L. Siri); Isabel I. (H. H. Keifer); Mazatlan (R. M. Bohart; P. J. Spangler); 20 mi S Villa Union (E. I. Schlinger); *Sonora*: Alamos (A. Mintzer); 4.8 mi S Cananea (V. Roth); Cocorit (F. D. Parker & L. A. Stange); 5 mi N Santa Cruz, 4700 ft (W. S. Creighton); *Tamaulipas*: Brownsville [= Matamoros?]; *Veracruz*: Cordoba; Jalapa (N. L. H. Krauss); La Buena Ventura (A. Petrunkewitch); Los Tuxtlas (R. L. Jeanne); Mirador (E. Skwarra); Veracruz; *state unknown*: Tetela [Oaxaca or Puebla].

BAHAMAS: Mangrove Cay, Andros I. (W. M. Mann); Nassau (W. M. Wheeler); San Salvador I. (J. F. Lynch); South Bimini I. (C. & P. Vaurie); Watlings I (J. Greenway).

BELIZE: Augustine (J. Reiskind); Rideau Camp (P. Broomfield).

COSTA RICA: *Cartago Prov.*: Cartago (N. L. H. Krauss); *Paraíso* (N. L. H. Krauss); *Guanacaste Prov.*: 15 km SW Bagaces, Comelco (H. V. Daly); Finca la Pacifica, 7 km SW Cañas (H. V. Daly); Hacienda la Pacifica, nr. Cañas, 50 m (P. S. Ward); 1 km SW Pto. Coyote, < 5 m (P. S. Ward); Santa Rosa Natl. Pk., < 5 m, 270 m (P. S. Ward); *Limon Prov.*: Linda Vista, 540 m (P. S. Ward); Puerto Viejo, < 5 m (P. S. Ward); *Puntarenas Prov.*: Monteverde (H. V. Daly); Monteverde, 1220 m, 1350 m, 1400 m (P. S. Ward); *San José Prov.*: 1 km N La Ese, 1400 m (P. S. Ward); Pavas, 1000 m (P. S. Ward); San José (W. M. Wheeler); Hamburg Farm (F. Nevermann).

CUBA: Santa Barbara, Isla de Pinos (S. C. Bruner).

EL SALVADOR: Cerro Verde (L. J. Bottimer); La Libertad (N. L. H. Krauss); San Salvador (L. J. Bottimer).

GUATEMALA: Antigua (W. M. Wheeler); San Lucas, Toliman (W. M. Wheeler).

HONDURAS: La Ceiba (F. J. Dyer).

Pseudomyrmex seminole Ward, *sp. nov.*

(Figs. 18, 21, 28, 44, 45)

Pseudomyrma flavidula; Wheeler (nec F. Smith), 1905, pp. 83–85 (partim).

Pseudomyrma pallida; Wheeler (nec F. Smith), 1932, p. 4 (partim).

Holotype worker: John Pennekamp State Pk., Munroe Co., Florida, < 5 m, 14.ix.1982, ex colony in dead *Andropogon* culm, roadside near mangrove, P. S. Ward acc. no. 5723 (MCZ). HW 0.90, HL 1.05, EL 0.50, PL 0.59, PH 0.29.

Paratype workers, queens, males: Two nest series from John Pennekamp St. Pk., Munroe Co., Florida, 14.ix.1982, ex dead *Andropogon* culms, P. S. Ward acc. nos. 5722, 5723; two nest series and ground foragers from 12 mi N. Key Largo, Munroe Co., Florida, 10.i.1979, ex dead *Andropogon* culms, and foraging on ground, P. S. Ward acc. nos. 3199, 3202, 3203 (BMNH, LACM, MCZ, PSW, UCD, USNM).

Type series is restricted to material from these two adjacent localities. Other specimens believed to be conspecific are listed below under "Material Examined".

Worker Measurements ($n = 26$): HL 0.98–1.16, HW 0.87–0.96, MFC 0.029–0.042, CI 0.81–0.89, OI 0.57–0.63, REL 0.43–0.48, REL2 0.53–0.56, OOI 1.04–1.94, VI 0.75–0.85, FCI 0.031–0.47, SI 0.42–0.47, SI2 0.75–0.85, FI 0.38–0.44, PDI 1.05–1.40, MPI 0.017–0.045, NI 0.53–0.62, PLI 0.46–0.53, PWI 0.39–0.47, PPWI 0.93–1.09.

DPL 0.75–0.87, MP 0.015–0.042, CDI 0.040–0.064, PLI2 1.11–1.34, PHI 0.56–0.67, PWI2 0.50–0.59, PPWI2 0.48–0.57.

Worker Diagnosis.— Relatively large species, with broad head (HW 0.87–0.96, CI 0.81–0.89); median portion of anterior clypeal margin obtusely (and weakly) angulate, sharply angulate laterally (Figure 44); distance between frontal carinae subequal to, or slightly less than, basal width of scape; eyes relatively short (REL 0.43–0.48); occipital margin convex or flat, in full face, dorsal view; lateral margins of pronotum rounded; metanotal groove wide but shallow; basal face of propodeum rounding into declivitous face, the former equal to, or longer than, the latter; petiole and postpetiole long and slender, the former with a distinct anterior peduncle and (usually) prominent, rounded anteroventral tooth. Mandibles very weakly striate, with scattered punctures; head subopaque to sublucid, densely punctulate on a coriarius background; mesosoma and petiole subopaque, coriarius-punctulate, becoming coriarius-imbricate laterally; postpetiole and gaster subopaque, with numerous fine piligerous punctures. Erect pilosity sparse, lacking on mesonotum and propodeum; one to several pairs of erect setae on dorsum of head, pronotum, petiole, postpetiole and abdominal tergite IV. Fine appressed hairs present on most parts of body, and forming a rather dense mat on abdominal tergite IV. Body orange brown; mandibles and apices of appendages variably paler.

Comments.— Essentially a Gulf Coast species, *P. seminole* occurs sympatrically with the closely related *P. pallidus*. Workers of *P. seminole* may be recognized by the less convergent

frontal carinae ($MFC \geq 0.029$ in *P. seminole*, ≤ 0.024 in *P. pallidus*), shorter eyes, and weakly angulate median portion of the anterior clypeal margin (compare Figures 42 and 44). The angulate clypeus of *P. seminole* tends to be a little more produced than that of *P. pallidus* workers ($CDI\ 0.040\text{--}0.064$ in *P. seminole*, $0.030\text{--}0.054$ in *P. pallidus*). On average, the petiole and postpetiole of *P. seminole* are longer and more slender than those of *P. pallidus*, but there is sufficient variation in both species that the relevant metrics overlap broadly. Differences between the queens of the two species are more pronounced and the male genitalia of *P. seminole* are quite distinct (see keys to queens and males).

Biology.— I have collected nests of *P. seminole* in dead stalks or culms of *Andropogon*, *Heterotheca subaxillaris*, *Uniola paniculata*, and an unidentified woody legume. None of these nests was polygynous; some were queenless, indicating that this species is polydomous.

On Padre Island, east Texas *P. seminole* is patchily distributed in a continuous population of *P. pallidus*. Both species use the same nest sites (*Heterotheca* stalks and *Uniola* culms). I have observed incipient *P. seminole* colonies consisting of (i) a single, dealate queen, (ii) a single, dealate queen with brood, and (twice) (iii) a single dealate queen in association with *P. pallidus* workers. In one of the latter instances a dealate *P. pallidus* queen and five workers occupied one *Uniola* internode, while the *P. seminole* queen occupied an adjacent cavity; in the second instance, the *P. seminole* queen coexisted with seven *P. pallidus* workers (but no queen) plus brood of unknown identity, in a single dead *Heterotheca* stalk. These observations suggest that *P. seminole* may be a facultative, temporary social parasite of *P. pallidus*.

Alates or alate pupae have been collected in most months of the year, indicating a rather continual production of sexuals.

Material Examined (BMNH, GCW, LACM, MCZ, PSW, UCD, USNM).—

FLORIDA: *Alachua Co.*: Gainesville (R. W. Klein); no specific locality (T. H. Hubbell); *Dade Co.*: Agric. Res. Educ. Centre, Homestead (R. W. Klein); Homestead Air Force Base (G. C. & J. Wheeler); Paradise Key (H. & A. Howden); *De Soto Co.*: Prairie Creek, 11 mi S. Arcadia (M. Deyrup); *Highlands Co.*: Highlands Hammock St. Pk. (C. W. O'Brien); *Hillsborough Co.*: no specific locality (B. P. Moore); *Indian River Co.*: Vero Beach (L. & C. W. O'Brien); *Monroe Co.*: John Pennekamp St. Pk. < 5 (P. S. Ward); Key Largo (A. C. Cole); 12 mi N Key Largo (P. S. Ward); *Osceola Co.*: Kissimmee; *Pinellas Co.*: Dunedin (Blatchley); *Polk Co.*: Lakeland (W. T. Davis).

LOUISIANA: *East Baton Rouge Co.*: Baton Rouge (M. R. Smith); *Iberia Co.*: New Iberia (A. H. Sturtevant).

MISSISSIPPI: *Harrison Co.*: Gulfport.

TEXAS: *Cameron Co.*: Brownsville (J. Knoll); *Nueces Co.*: Mustang I. St. Pk. (P. S. Ward); Port Aransas, 5 m (P. S. Ward); 3.4 km SW Port Aransas, 5 m (P. S. Ward); 11 km SW Port Aransas, 5 m (P. S. Ward).

MEXICO: *Tamaulipas*: 7 km WSW El Encino, 140 m (P. S. Ward)

BAHAMAS: Nassau (W. M. Wheeler).

Pseudomyrmex simplex F. Smith

(Figs. 22, 29, 40, 41)

Pseudomyrma simplex F. Smith 1877, p. 64. Holotype (unique syntype) worker, São Paulo ["St. Paul"], Brazil (BMNH) [Examined].

Pseudomyrma delicatula Forel, 1899, p. 93. Syntype workers, one dealate queen, Kingston, Jamaica (Forel) (MHN) [Examined.] *Syn. nov.*

Pseudomyrma delicatula var. *panamensis* Forel, 1899, p. 93. Holotype (unique syntype) worker, Pantaleon, Guatemala, 1700 ft (Champion) (MHN) [Examined]. *Syn. nov.*

Pseudomyrma delicatula var. *capperi* Forel, 1899, p. 93. Syntype workers, Jamaica (Capper) (MHN) [Examined]. *Syn. nov.*

Pseudomyrma acanthobia race *delicatula*, var. *vittata* Forel, 1912, p. 26. Syntype workers, Ceara, Brazil (Rocha) (MHN) [Examined]. *Syn. nov.*

Pseudomyrma flavidula var. *delicatula* Forel; Wheeler, 1913, p. 484.

Pseudomyrma flavidula var. *delicatula* Forel; Wheeler & Mann, 1914, p. 17.

Pseudomyrma flavidula; Wheeler (nec F. Smith), 1932, p. 4 (partim).

Pseudomyrma pallida; Creighton (nec F. Smith), 1950, pp. 80–82 (partim).

Pseudomyrmex pallidus Wilson (nec F. Smith), 1964, pp. 4–5 (partim).

Worker Measurements ($n = 46$): HL 0.70–0.92, HW 0.55–0.74, MFC 0.009–0.017, CI 0.75–0.85, OI 0.49–0.55, REL 0.52–0.61, REL2 0.62–0.77, OOI 0.55–1.92, VI 0.68–0.83, FCI 0.013–0.025, SI 0.40–0.48, SI2 0.56–0.72, FI 0.45–0.52, PDI 1.27–1.94, MPI 0.005–0.043, NI 0.53–0.65, PLI 0.50–0.69, PWI 0.39–0.60, PPWI 0.97–1.31.

Worker Diagnosis.— Relatively small species, with moderately elongate head (HW 0.55–0.74, CI 0.75–0.85); median portion of anterior clypeal margin straight, laterally angulate; frontal carinae very closely contiguous (minimum distance between them much less than the basal width of scape); eyes relatively long (REL 0.52–0.61); occipital margin concave, flat, or slightly convex, in full face, dorsal view; lateral margins of pronotum rounded; metanotal groove very weak and shallow; basal face of propodeum longer than declivitous face, and more or less clearly differentiated from it; petiole relatively short, with an anterior peduncle and anteroventral tooth; postpetiole often wider than long, somewhat globose in lateral view. Head predominately smooth and shining; frons with scattered fine punctures of variable size, on a smooth or obsoletely coriarius background; punctures less dense on the vertex, which is smooth and shining; mesosoma and petiole sublucid, dorsally weakly coriarius-punctulate, laterally coriarius-imbricate; postpetiole and gaster more or less smooth and shining. Erect pilosity sparse, lacking on mesonotum, propodeum, mid and hind femora, and (often) petiole; typically a pair of erect setae on pronotum, postpetiole, and adjacent to the eyes. Fine, appressed pubescence very sparse, notably so on postpetiole and abdominal tergite IV. Light orange brown, mandibles and clypeus a paler luteous; a pair of anterolateral fuscous patches usually present (sometimes weak) on abdominal tergite IV.

Comments.— This species is the smallest one of a trio of orange *Pseudomyrmex* (*P. pallidus*, *P. seminole*, *P. simplex*) which have been confused repeatedly in the United States. *P. simplex* workers are recognizable by their smooth, shiny, punctulate head; broad forefemur ($FI \geq 0.45$); and shining fourth abdominal tergite which is devoid of a dense mat of appressed pubescence. In addition the workers have long eyes, closely contiguous frontal carinae, a very shallow metanotal groove, and a short petiole and postpetiole. The *simplex* and *delicatulus* types share these essential features, along with the other material which I have examined. There is a fair range of variation in size and body proportions (see metrics). *P. simplex* tends to be lighter in color than related species, and the fuscous patches on abdominal tergite IV are usually conspicuous, at least in Florida populations (less so in Central and South America).

Biology.— *P. simplex* shows a preference for nesting in dead twigs of woody shrubs or trees, rather than in dead stalks of herbaceous plants. In Florida, I have collected nests in dead twigs or stalks of *Baccharis halimifolia*, *Cladium jamaicense*, *Laguncularia racemosa*, *Metopium toxiferum*, and *Nectandra coriacea*; there are also museum records from *Carya floridana* and *Swietenia mahagoni*.

In Costa Rica I recorded nests of *P. simplex* in dead twigs of *Anacardium*, *Ardisia revoluta*, *Avicennia germinans*, *Conocarpus erectus*, *Gliricidia sepium*, *Hibiscus tiliaceus*, and *Terminalia catappa*.

Most *P. simplex* nests I dissected were queenless (indicating a high level of polydomy), some were monogynous, and one contained two functional (i.e. inseminated, with well-developed ovaries) tealate queens.

Alates have been collected in May, June, and September in Florida.

Material Examined (BMNH, GCW, LACM, MCSN, MCZ, MHN, NHMB, PSW, UCD, USNM).—

FLORIDA: *Charlotte Co.*: Punta Gorda (W. T. Davis); *Collier Co.*: Marco (W. T. Davis); *Dade Co.*: Biscayne Bay (A. Slosson); Long Pine Key, Everglades Natl. Pk., 10 m (P. S. Ward); Mahogany Hammock, Everglades Natl. Pk. (G. C. & J. Wheeler); Miami (G. B. Merill; C. F. W. Muesebeck; C. Stegmaier); Paradise Key (H. S. Barber); Pinelands Trail, Everglades Natl. Pk. (G. C. & J. Wheeler); no specific locality (J. N. Knoll); *Highlands Co.*: Archbold Biol. Stn., Lake Placid (J. Walker); *Monroe Co.*: Big Pine Key (P. S. Ward; E. O. Wilson) John Pennekamp St. Pk., < 5 m (P. S. Ward); N Key Largo (R. W. Klein); 16 mi N Key Largo (P. S. Ward); Refuge Nature Trail, Big Pine Key, 10 m (P. S. Ward); Key West; *Pinellas Co.*: Dunedin (Blatchley); *Sarasota Co.*: Long Branch Key, Sarasota (Cole).

MEXICO: *Quintana Roo*: San Miguel, Cozumel I. (N. L. H. Krauss); *Tamaulipas*: Tampico (F. C. Bishop).

BAHAMAS: Gun Point, Crooked I. (B. Valentine & A. Hamilton); Mangrove Cay, Andros I. (B. Cole); New Providence (B. Cole).

BELIZE: Belize (N. L. H. Krauss); El Cayo (N. L. H. Krauss); Punta Gorda (P. Broomfield).

CAYMAN IS.: Grand Cayman (M. E. C. Giglioli)

COSTA RICA: *Guanacaste Prov.*: Hacienda la Pacifica, nr. Cañas, 50 m (P. S. Ward); 1 km SW Pto. Coyote, < 5 m (P. S. Ward); Santa Rosa Natl. Pk., < 5 m, 5 m, (P. S. Ward); Taboga Hill (C. R. Carroll); *Limon Prov.*: Cahuita Natl. Pk., < 5 m (P. S. Ward); *Puntarenas Prov.*: Lagarto, 120 m (P. S. Ward); Llorona, Corcovado Natl. Pk., 10 m (P. S. Ward); Manuel Antonio Natl. Pk. 5 m, 20 m (P. S. Ward); Osa Peninsula, Corcovado (J. Longino); *San José Prov.*: San José (W. M. Wheeler); *province unknown*: "Costa Rica" (Tonduz).

CUBA: Cogimar (W. M. Wheeler); Yunque, Baracoa, Ote (P. J. Darlington).

EL SALVADOR: Quezaltepeque (M. Irwin & D. Cavagnaro).

GUATEMALA: Escuintla (P. J. Spangler); Livingston (Barber & Schwartz); Pantaleon (Champion); "Guatemala" (Stoll).

HAITI: Cape Haitien (W. M. Mann).

HONDURAS: La Ceiba (F. J. Dyer); Tegucigalpa (F. J. Dyer).

JAMAICA: Balaclava (Wight); Kingston (A. Forel; P. Vogel); Lapland, Catadupa; Mandeville (Wight); Montego Bay; "Jamaïque" (Capper).

PANAMA: Ancon, Canal Zone (W. M. Wheeler); Barro Colorado I., Canal Zone (W. L. Brown and E. S. McCluskey; Zetek); Cristobal, Canal Zone (H. F. Dietz); 2 km SE Fort Kobbe, Canal Zone, 10 m (P. S. Ward); 5 km WNW Gatun Dam, Canal Zone, 160 m (P. S. Ward).

PUERTO RICO: Mayagüez (M. R. Smith).

TRINIDAD: Port of Spain (R. Thaxter); St. George (J. Noyes).

WEST INDIES: St. Lucia (N. A. Weber).

BRAZIL: *Amazonas*: Rio Taruma Mirim-Igapó (J. Adis); *Bahia*: Bondaz; *Ceara*: no specific locality (Rocha); *Pará*: Ourem; Santarem, Taperinha (R. L. Jeanne); Tacura; Tucurul (W. L. Overal); *Paraná*: Independencia (Mann & Heath); *Rio de Janeiro*: Mendes (Eidmann); *São Paulo*: São Paulo.

COLOMBIA: Huila (B. & E. MacKay); Serrania de Macuira, 6-8 km S. Nazareth, 70-200 m (W. L. Brown & R. C. Kugler).

ECUADOR: Rio Palenque (L. Gillespie).

PERU: Piura (Townsend).

DISCUSSION

Coexistence of congeners

Every Nearctic species of *Pseudomyrmex* occurs sympatrically with two or more congeners in at least some portion of its range. Where two or more species co-occur, they often use a broadly overlapping array of nest-sites. For example, in the Florida Keys, *Cladium* culms are occupied by both *P. pallidus* and *P. simplex*, although *P. simplex* also nests in woody twigs, and *P. pallidus* will nest in *Andropogon* culms (a nest-site shared with *P. seminole*); on Padre Island, east Texas *P. pallidus* and *P. seminole* occupy the same nest-sites (*Uniola* culms and *Heterotheca* stalks); in northern Mexico, *P. ejectus* and *P. brunneus* were both recorded nesting in dead mint stalks at the same location. In none of the above instances were workers of the coexisting species found together in the same *individual* nest-site, but they could be found in adjacent stalks separated by only a few meters. The impression to be gained from these field observations is that there is a rather high degree of overlap among related species using the dead stalks or culms of *herbaceous* plants. These nest-sites can be expected to have a short half-life, relative to dead woody twigs or branches. The ephemeral nature and continual production of such sites may allow the coexistence of nest-site competitors, in a manner analogous to competing fish on coral reef patches (Sale, 1977).

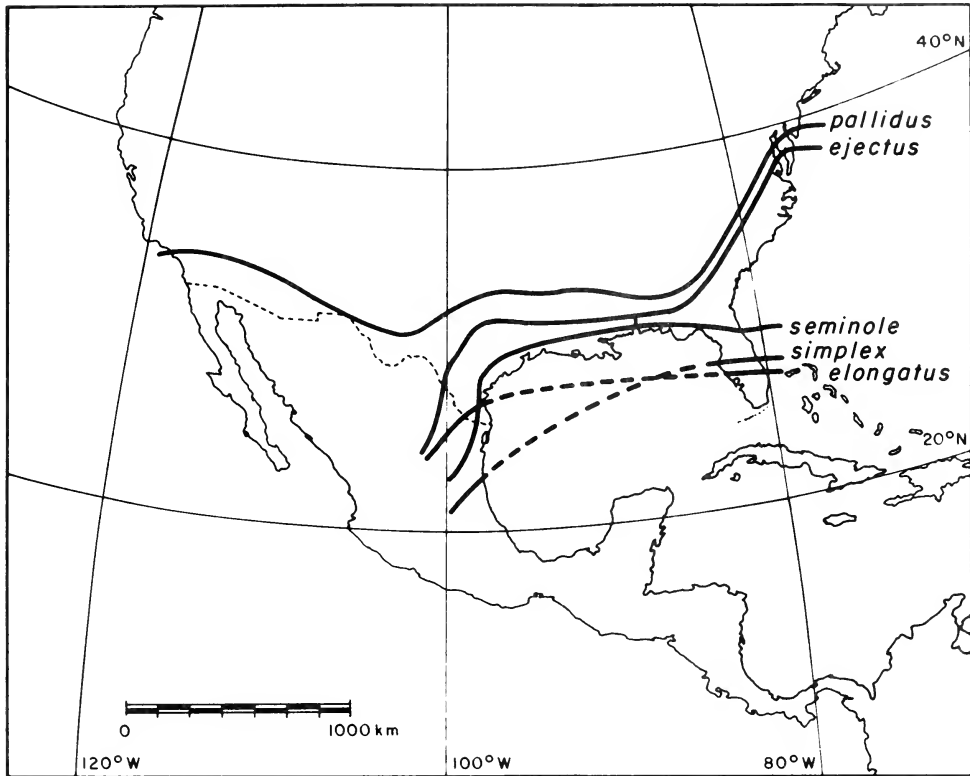


Figure 46. Northern limits of some Nearctic *Pseudomyrmex*. All of these species, except *P. seminole*, range south through Central America.

Geographical distribution and speciation

Although most Nearctic *Pseudomyrmex* species show extensive overlap of their geographical ranges, each species has a rather distinctive northern limit (Figure 46). This variable penetration into North America of essentially Neotropical taxa results in a gradient of species diversity which is maximal in southern Texas and southern Florida. The disjunct distributions across the Gulf of Mexico suggest a possible basis for previous differentiation and speciation. Thus *P. cubaensis* may represent an earlier Florida-Antillean isolate cut off from Central American populations of *P. elongatus* by a cooling trend. By this interpretation, contemporary populations of *P. elongatus* in Florida and Texas (which show some morphological differentiation) represent the severance of a more recent Gulf Coast connection.

Other closely related species of Nearctic *Pseudomyrmex* have rather different distribution patterns. In three cases, the range of one member of a sibling species pair is rather limited in

extent and is completely enclosed within the range of the other member (*P. brunneus* by *P. ejectus*, *P. leptosus* by *P. pallidus*, *P. seminole* by *P. pallidus*). This suggests that the more localized species was derived from a divergent, daughter population of the widespread species (Type 1b allopatric speciation in the parlance of Bush (1975)). One might even question whether the differentiation always proceeded allopatrically, since *P. seminole* shows evidence of being a temporary social parasite of *P. pallidus*, its presumptive ancestor. Moreover the social parasitic species *P. leptosus* is very localized and is surrounded by, sympatric with, and morphologically similar to *P. pallidus* (although its only known host is *P. ejectus*, a less closely related species). In any event, differentiation to the point of attaining reproductive isolation appears to be a plausible event on both a local and a broad geographical scale.

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Appendix 1. *Pseudomyrmex* queens and males. Ranges of metric measurements and indices.

Queens	<i>mexicanus</i>	<i>cubaensis</i>	<i>elongatus</i>	<i>apache</i>	<i>brunneus</i>	<i>ejectus</i>	<i>leptotus</i>	<i>pallidus</i>	<i>seminole</i>	<i>simplex</i>
HL	1.56-1.98	1.02-1.23	0.91-0.96	1.28-1.46	0.83	0.86-0.99	0.83-0.91	0.82-1.15	1.31-1.42	0.80-1.02
HW	1.52-1.76	0.65-0.72	0.56-0.59	0.85-1.02	0.67	0.62-0.75	0.67-0.70	0.66-0.92	0.96-1.03	0.57-0.75
MFC	.039-.062	.021-.038	.016-.032	.053-.095	.010	.011-.018	.019-.027	.016-.035	.065-.075	.008-.021
CI	0.89-0.98	0.57-0.64	0.59-0.64	0.66-0.75	0.81	0.73-0.79	0.77-0.82	0.68-0.86	0.72-0.76	0.69-0.77
OI	0.46-0.51	0.52-0.54	0.49-0.55	0.57-0.63	0.54	0.51-0.60	0.53-0.59	0.51-0.60	0.55-0.62	0.49-0.54
REL	0.55-0.60	0.43-0.47	0.48-0.53	0.37-0.40	0.54	0.50-0.54	0.47-0.51	0.45-0.51	0.41-0.43	0.49-0.57
REL2	0.59-0.65	0.68-0.80	0.77-0.89	0.52-0.58	0.67	0.67-0.71	0.59-0.63	0.59-0.71	0.55-0.57	0.65-0.80
OOI	(-0.25)-0.35	0.33-0.82	0.07-0.30	1.08-1.56	1.10	0.59-1.02	0.92-1.58	0.55-1.54	0.77-1.16	0.47-1.01
VI	0.73-0.89	0.85-0.93	0.89-0.93	0.84-0.91	0.71	0.74-0.85	0.68-0.75	0.71-0.88	0.90-0.93	0.80-0.88
FCI	.024-.038	.031-.053	.029-.055	.052-.094	.015	.015-.026	.028-.039	.022-.046	.066-.075	.014-.029
SI	0.46-0.49	0.47-0.50	0.45-0.49	0.46-0.50	0.45	0.43-0.49	0.45-0.48	0.42-0.53	0.39-0.45	0.41-0.47
SI2	0.72-0.79	0.61-0.71	0.55-0.62	0.85-0.94	0.67	0.63-0.72	0.75-0.77	0.64-0.79	0.70-0.80	0.52-0.68
FI	0.39-0.45	0.44-0.53	0.46-0.51	0.42-0.46	0.50	0.45-0.52	0.42-0.47	0.42-0.54	0.46-0.53	0.49-0.55
NI	0.60-0.68	0.61-0.69	0.58-0.67	0.57-0.66	0.66	0.60-0.68	0.60-0.68	0.56-0.67	0.63-0.66	0.61-0.71
PLI	0.48-0.52	0.58-0.67	0.66-0.76	0.49-0.57	0.48	0.43-0.48	0.47-0.51	0.44-0.58	0.43-0.49	0.48-0.55
PWI	0.44-0.52	0.57-0.66	0.60-0.68	0.54-0.60	0.48	0.42-0.48	0.43-0.51	0.40-0.55	0.41-0.51	0.42-0.54
PPWI	1.05-1.25	1.16-1.25	1.17-1.41	1.15-1.28	1.26	1.00-1.12	1.02-1.18	0.97-1.23	1.00-1.11	0.99-1.23
sample size	9	10	5	10	1	13	11	30	10	17

(continued on next page)

Appendix 1 (continued)

Males

	<i>mexicanus</i>	<i>cubaensis</i>	<i>elongatus</i>	<i>apache</i>	<i>brunneus</i>	<i>ejectus</i>	<i>leptosus</i>	<i>pallidus</i>	<i>seminole</i>	<i>simplex</i>
HL	1.25-1.37	1.08-1.22	0.80-0.88	0.91-1.08	-	0.75-0.92	0.68-0.77	0.72-0.97	0.89-1.07	0.73-0.93
HW	1.32-1.52	0.76-0.82	0.59-0.62	0.82-0.98	-	0.66-0.77	0.61-0.68	0.67-0.84	0.81-0.92	0.58-0.78
MFC	0.27-0.31	0.13-0.17	0.08-0.12	0.15-0.20	-	0.11-0.12	0.10-0.11	0.12-0.16	0.12-0.16	0.09-0.16
CI	1.10-1.14	0.65-0.71	0.69-0.76	0.85-0.95	-	0.78-0.88	0.88-0.89	0.82-0.96	0.85-0.91	0.78-0.88
OI	0.51-0.56	0.57-0.63	0.58-0.64	0.63-0.71	-	0.62-0.68	0.52-0.64	0.59-0.69	0.67-0.72	0.58-0.68
REL	0.60-0.63	0.49-0.51	0.55-0.58	0.47-0.49	-	0.50-0.55	0.51-0.62	0.50-0.58	0.49-0.53	0.52-0.60
REL2	0.53-0.57	0.71-0.77	0.73-0.83	0.50-0.57	-	0.61-0.67	0.59-0.71	0.58-0.64	0.56-0.59	0.61-0.76
OOI	(-0.10)-0.17	0.13-0.44	0.06-0.22	0.22-0.93	-	0.18-0.48	(-0.17)-0.73	0.11-0.68	0.29-0.54	(-0.09)-0.38
VI	0.60-0.67	0.57-0.62	0.54-0.62	0.55-0.67	-	0.53-0.64	0.50-0.56	0.47-0.60	0.57-0.62	0.53-0.64
FCI	0.20-0.20	0.17-0.22	0.14-0.19	0.18-0.21	-	0.15-0.17	0.16-0.18	0.16-0.20	0.15-0.17	0.15-0.21
SI	0.16-0.18	0.26-0.28	0.22-0.25	0.22-0.27	-	0.29-0.33	0.30-0.32	0.27-0.33	0.28-0.32	0.25-0.31
SI2	0.30-0.33	0.36-0.38	0.30-0.34	0.43-0.51	-	0.45-0.52	0.42-0.55	0.44-0.54	0.47-0.57	0.36-0.47
SI3	0.57-0.68	0.77-0.89	0.68-0.80	0.75-0.96	-	0.80-1.02	1.11-1.25	0.80-1.13	0.70-0.97	0.78-0.98
FI	0.31-0.33	0.35-0.38	0.32-0.38	0.25-0.29	-	0.30-0.36	0.26-0.28	0.29-0.35	0.30-0.36	0.36-0.51
NI	0.73-0.75	0.66-0.73	0.62-0.69	0.61-0.74	-	0.63-0.68	0.60-0.65	0.63-0.72	0.61-0.67	0.63-0.73
PLI	0.29-0.36	0.45-0.53	0.46-0.52	0.39-0.55	-	0.35-0.49	0.42-0.45	0.31-0.44	0.39-0.45	0.42-0.56
PWI	0.27-0.33	0.35-0.40	0.34-0.39	0.36-0.45	-	0.31-0.39	0.30-0.33	0.28-0.35	0.31-0.36	0.34-0.44
PPWI	0.72-0.80	0.72-0.85	0.68-0.79	0.86-0.99	-	0.71-0.87	0.70-0.82	0.69-0.90	0.69-0.85	0.77-0.93

sample
size

4 6 7 9 - 7 5 12 6 11



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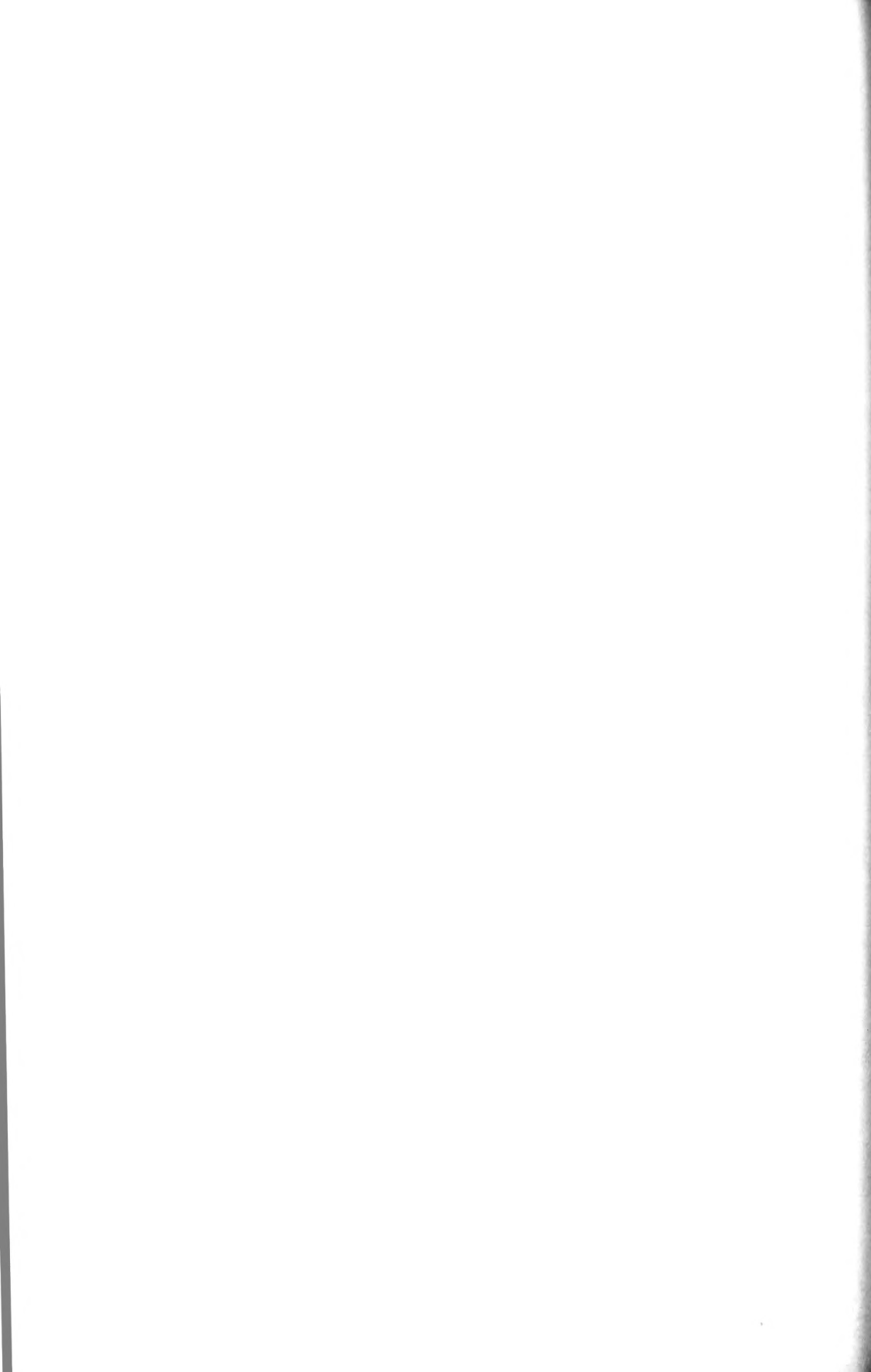
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TAXONOMY, PHYLOGENY AND BIOGEOGRAPHY OF THE CARRION BEETLES OF LATIN AMERICA (COLEOPTERA: SILPHIDAE)

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ABSTRACT

The species of Silphidae, excluding Agyrtidae, are reviewed for Mexico, Central America, and South America. Keys are provided for the identification of adults of six genera (Necrodes, Heterosilpha, Oiceoptoma, Thanatophilus, Oxelytrum, Nicrophorus) and 24 species known or suspected to occur in Mexico or southward. No new species are proposed. The following new synonymies are presented: Silpha microps Sharp is a junior synonym of Oxelytrum anticola (Guérin-Méneville) and Hyponecrodes opacus Portevin is a junior synonym of Oxelytrum erythrurum (Blanchard).

Given for each species, as appropriate, are: synonymy, diagnosis, comments on variation, geographic distribution, seasonality, ecological data, and illustrations of important structural characteristics. Geographic distributions are mapped for all species.

Oxelytrum is regarded as the sister genus to Ptomaphila of the Australian region. Oxelytrum, represented by eight species, probably originated and diversified during the Tertiary in South America when this continent was isolated. Two lineages of Oxelytrum are recognized based on adult characters. The emarginatum group has four species found in northern and eastern lowland and mid-elevation montane habitats, with only one species, O. discicolle, ranging into Central America and north to extreme southern Texas. The lineatocolle group has four species found in south-western coastal lowlands and low to high elevation montane habitats.

Nearctic species of Necrodes, Oiceoptoma, Heterosilpha and Thanatophilus which also occur in Latin America range no further south than the Isthmus of Tehuantepec. Only T. graniger is endemic, found in high elevation habitats of central and northern Mexico.

Nicrophorus is represented by nine species in three species groups in Latin America. All groups are of northern origin. The five species of Nicrophorus endemic to Latin America are all members of the orbicollis group. Ancestors of the three South American endemic species probably moved south along the mountain axis of Central and South America in late Cretaceous or early Tertiary time and likely diversified in the Tertiary following fragmentation of forest habitats. The two Middle American endemics are probably the result of a second, but mid-Tertiary, inter-island dispersal of a northern ancestor. The four remaining species of Nicrophorus represent two species groups. All of these species occur in the United States with three ranging into arid areas of central and northern Mexico; the

fourth ranges south to El Salvador.

A classification of New World Nicrophorus is also presented. Thirteen of the fifteen New World species are placed in four species groups based on larval and adult characters. Two species are Incertae sedis. A reconstructed phylogeny is presented for the New World members of each species group.

RESUMEN

Se revisan las especies de Silphidae, excluyendo Agyrtidae, de México, Centroamérica y Suramérica. Se proveen claves para la identificación de los adultos de los 6 géneros (Necrodes, Heterosilpha, Oiceoptoma, Thanatophilus, Oxelytrum, Nicrophorus) y 24 especies que se conoce o se sospecha que existen en México o hacia el sur. No se proponen nuevas especies. Se presentan, a continuación, los nuevos sinónimos: Silpha microps Sharp es un sinónimo reciente de Oxelytrum anticola (Guérin-Mèneville) e Hyponecrodes opacus Portevin es un sinónimo reciente de Oxelytrum erythrurum (Blanchard).

Se dan para cada especie, según sea apropiado: la sinonimia, el diagnóstico, comentarios sobre la variación, la frecuencia por estación, datos ecológicos e ilustraciones de características estructurales importantes. Se presentan las distribuciones geográficas de todas las especies.

Oxelytrum se considera el género hermano de Ptomaphila de la región australiana. Oxelytrum, representado por ocho especies, probablemente se originó y diversificó en Suramérica durante el Terciario cuando este continente se encontraba aislado. Basados en las características de los adultos, se reconocen dos linajes en Oxelytrum. El grupo emarginatum tiene 4 especies que se encuentran en hábitats montanos de baja y media altitud en el este y norte de Norteamérica, con una sola especie, O. discicolle, que se extiende a Centroamérica y de allí hacia el norte hasta el extremo sur de Texas. El grupo lineatocolle tiene 4 especies que se encuentran en áreas de baja elevación en la costa suroeste y en hábitats montanos de alta y baja altitud.

Las especies neárticas Necrodes, Oiceoptoma, Heterosilpha y Thanatophilus que también se presentan en Latinoamérica se extienden, hacia el sur, no más allá del Istmo de Tehuantepec. T. graniger es la única endémica, encontrándose en hábitats de alta elevación en el centro y norte de México.

Nicrophorus está representado por 9 especies en 3 grupos de especies. Todos los grupos tienen su origen en el norte. Las 5 especies de Nicrophorus, endémicas para Latinoamérica, son todas miembros del grupo orbicallis. Los ancestros de las 3 especies endémicas de suramérica probablemente se dispersaron al sur a través del eje montañoso de Centro y Sur América en el Cretáceo tardío o a comienzos del Terciario y, es muy posible, que se diversificaran en el Terciario, siguiendo la fragmentación de los hábitats forestales. Las dos endémicas de Mesoamérica son, probablemente, el resultado de una dispersión secundaria a través de islas, a partir de un ancestro norteño durante el Terciario medio. Las cuatro especies restantes de Nicrophorus representan dos grupos de especies. Todas estas especies se encuentran en los Estados Unidos con tres que se extienden hasta zonas áridas del centro y norte de México; la cuarta, se extiende, hacia el sur, hasta El Salvador.

Se presenta también una clasificación de Nicrophorus para el Nuevo Mundo. Trece de las quince especies del Nuevo Mundo se agrupan en 4 grupos de especies basados en caracteres de las larvas y los adultos. Dos especies son Incertae sedis. Se presenta una reconstrucción filogenética para los miembros de cada grupo de especies del Nuevo Mundo.

INTRODUCTION

The Silphidae, or carrion beetles, are the predominant beetles scavenging on dead terrestrial vertebrate remains in temperate and sub-arctic regions in the Northern Hemisphere. Silphids also occur in tropical lowlands, as well as in tropical montane and south temperate regions. However, their role in the carrion-feeding insect guild is noticeably less in tropical than in temperate regions (Cornaby, 1974; Jirón and Cartín, 1981). They are probably less abundant in lowland tropical regions because they are less able to compete with increased rates of bacterial decomposition and feeding of ants and fly larvae, and with the greater abundance of carrion scavenging vertebrates (Arnett, 1946; Janzen, 1976). Recent reviews of the silphid fauna of North America north of Mexico recognized 29 species in 8 genera (Anderson and Peck, 1985), most of which have their relationships with species in Europe and Asia. Some of these also have distributions extending south into Mexico. However, most of the Latin American (used herein to indicate all of Mexico, Central America, and South America) fauna

consists of species in the primarily South American genus *Oxelytrum* and of endemic species in the genus *Nicrophorus*. No silphids are known to occur on the islands of the Caribbean.

The Latin American silphids were last revised by Portevin (1926). His liberal use of infraspecific categories, inadequately illustrated and complex keys, which also served as descriptions, and vague distributional data have led to problems in interpreting the species in Latin America. This present work attempts to alleviate these problems by reviewing and revising available knowledge about classification, distribution, and relationships of the Latin American silphid fauna.

NATURAL HISTORY

Silphid beetles are commonly called carrion beetles because of their association with dead vertebrate carcasses. Both adults and larvae of most species are scavengers and eat carrion. Based on studies of Nearctic species, silphids feed in two different ways. In the first, both adults and larvae of the sub-family Silphinae feed on comparatively large carcasses which remain exposed on the soil surface. No parental care of larvae is known. In the second, adults of the genus *Nicrophorus* feed at large and exposed carcasses, but they must also secure a comparatively small carcass and bury it for reproduction and subsequent larval maturation. Adults remain with the developing larvae and care for them until they pupate. The Oriental genus *Ptomascopus* exhibits behavior combining aspects of the life histories of both Silphinae and *Nicrophorus*, but does not exhibit the parental care of larvae typical of *Nicrophorus* (Peck, 1982). These differing methods of carrion use are also found in Palearctic Silphidae.

Detailed studies have not been made on the Neotropical species, but there is no reason to suspect that their feeding and reproductive behaviors differ. Our field observations indicate that all species of *Oxelytrum* behave as typical Silphinae in feeding and breeding primarily on large carcasses. Species of *Oxelytrum* differ from most Nearctic and Palearctic silphines in that most are nocturnal instead of being diurnal.

Unfortunately, natural history data are few for Latin American species of *Nicrophorus* but they indicate that at least some of the species are nocturnal. There is no reason to suspect that Latin American *Nicrophorus* differ in other aspects of their natural history from Holarctic *Nicrophorus*. Rearings have not been attempted, and larvae are unknown for most species.

Anderson (1982a, 1982b) and Anderson and Peck (1985) review more detailed accounts of the natural history of silphids.

METHODS

We do not include the Agyrtidae, previously considered as part of the Silphidae, but now separated as a distinct family (Lawrence, 1982; Lawrence and Newton, 1982). The only agyrtids known from Latin America are three Mexican species of *Apteroloma* (reviewed in Bolívar and Hendrichs, 1972, who list them as *Pteroloma*).

Full synonymies for North American genera and species are given in Peck and Miller (in press). Type-species of genus-group names are in Madge (1980). Full synonymies are not given here for species which also occur in the U.S. and Canada; they are given in Peck and Miller (in press), and Anderson and Peck (1985). Full synonymies are listed only for those species limited in their distribution to Latin America. All original literature has been checked unless otherwise noted. We give the first use of a name or combination, and only references that contribute new

data. It is not our intention to give references to every use of a name in the older literature. We do not cite "aberrations" but only usage of a name as a "variety", because it may be interpreted as having subspecific rank (International Code of Zoological Nomenclature, 1974, art. 45 (e) (i)). For species that occur in the U.S. and Canada as well as Latin America, only the synonyms pertaining to material from Latin America are given. *Nomina nuda* are not cited. Such are listed by Portevin (1926), Hatch (1928), and Blackwelder (1944). Depositories are indicated for type material we examined. In those instances where type material was not examined we have indicated the probable depository according to Horn and Kahle (1937), and noted this with a question mark.

Keys for identification of species north of Mexico were published by Miller and Peck (1979), Peck (in press), and Anderson and Peck (1985) and should be consulted to confirm species identifications of specimens from northern Mexico. Keys presented here include only species known or likely to occur in Latin America. Keys for larvae are not presented because of lack of species descriptions. Keys to larvae of some genera and species which occur in Latin America are in Anderson and Peck (1985).

Species that may in the future be found to naturally occur in Latin America, but are not yet recorded, are mentioned below. These are excluded from the detailed species discussions and keys.

Nicrophorus americanus, *N. carolinus*, *N. investigator*, and *N. tomentosus* and some silphines of the southeastern United States may yet be found in Mexico because they occur in bordering states to the north. A significant component of the biota of this region does occur in temperate forests in northeastern Mexico (Martin and Harrell, 1957; Rosen, 1978). We have seen one specimen of *N. sayi* labelled "Mexico, N.L., Sierra de Gaucamayaz, Zaragoza, 2-3.VII.69, J.M. Matthieu, M.W. Sanderson, trampa de luz negra" (SBPC) but cannot accept this single record for this far northern species as evidence of its occurrence in Mexico. Another doubtful record is one of *Necrophila americana* labeled "Cuepayaca" (Cuernavaca) IX-46, H. Field (FMNH).

Old records that we believe are erroneous, doubtful, or un-substantiated by recent specimens are cited in Portevin (1926), Hatch (1928), and Blackwelder (1944). We do not discuss these any further.

We have been unable to establish the identity of the names *Nicrophorus quadricollis* Gistel from Mexico and *Necrodes pronotus* Gistel (1857:94) from Brazil. The types were supposedly in the collections of the Zoological Museum in Munich (Horn and Kahle, 1937), but are now considered lost (G. Scherer, *in litteris* 1984).

Distributions of all species are mapped based on personal examination of specimens. Because of space limitations, full label data are not given but are available from the first author. We cite only condensed locality (under State or Department or Province names in large countries) and ecological data in alphabetical order, month (if on label) and number of specimens if more than one. Specimen repository information or literature references follow the records for each country. Obscure localities from Matthews (1888) in the *Biologia Centrali Americana* were verified or located in Selander and Vaurie (1962).

All drawings were prepared with a camera lucida or an ocular grid and squared paper. Measurements of length are from the anterior margin of pronotum to the elytral apex.

Phylogenies are reconstructed following Hennig (1966) and Wiley (1981). As do most systematists, we adopt the biological species concepts as outlined by Mayr (1963). Since there is no direct information available about reproductive isolation in Latin American Silphidae,

such isolation is inferred from differences in structural features, distribution, and available information about natural history. We do not attempt to recognize subspecies. Adequate population samples are not available to investigate the significance of variation in coloration such as occur in some species of *Oxelytrum* and *Nicrophorus*.

MATERIALS

We have borrowed and examined material, totaling more than 4580 specimens, from the following individuals and collections through the kindness of their owners or curators as follows:

- AFNC Alfred F. Newton, Jr. Collection, Cambridge, Mass., U.S.A.
- BMNH British Museum (Natural History), London; England; R.B. Madge.
- CASC California Academy of Sciences, San Francisco, California, U.S.A.; D.H. Kavanaugh.
- CBMV Carlos Bordon Collection, Maracay, Venezuela; C. Bordon.
- CMNH Carnegie Museum of Natural History, Pittsburg, Penn., U.S.A.; G. Ekis
- CNCI Canadian National Collection of Insects, Ottawa, Ont., Canada; A. Smetana.
- FMLC Fundacion M. Lillo, Tucuman, Argentina; R. Golbach.
- FMNH Field Museum of Natural History, Chicago, Ill., U.S.A.; H.S. Dybas.
- FSCA Florida State Collection of Arthropods, Gainesville, Fla., U.S.A.; R.E. Woodruff.
- GMNH Geneva Museum of Natural History, Geneva, Switzerland; I. Lobl.
- INPA Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil; N.D. Penny.
- ITMM Instituto Tecnológico de Monterrey, México; Juan Contreras.
- IZAV Instituto de Zoología Agrícola, Maracay, Venezuela; F. Fernandez-Yepey.
- LACM Natural History Musuem of Los Angeles County, Los Angeles, California, U.S.A.; C.L. Hogue.
- LPMCN La Plata Museo de Ciencias Naturales, La Plata, Argentina; L. De Santis.
- MCZC Musuem of Comparative Zoology, Harvard University, Cambridge, Mass., U.S.A.; A.F. Newton, Jr.
- MHNM Museo de Historia Natural de la Ciudad de México, México City, México; P. Reyes-Castillo.
- MNHN Museum National d'Histoire Naturelle, Paris, France; N. Berti.
- MNSC Museo Nacional de Historia Natural, Santiago, Chile; G.A. Santic.
- MZUSP Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil; C. Costa.
- OSCU Ohio State University, Department of Entomology, Columbus, Ohio, U.S.A.; C.A. Triplehorn.
- PURC Purdue University Entomology Collection, Lafayette, Ind., U.S.A.; R.D. Waltz.
- RDCC R.D. Cave Collection, Auburn, Ala., U.S.A.
- RSAC Robert S. Anderson Collection, Edmonton, Alta., Canada.
- SDMC San Diego Natural History Musuem, San Diego, Calif., U.S.A.; S.E. Miller.

SBPC	Stewart B. Peck Collection, Ottawa, Ont., Canada.
TMMC	Texas Memorial Museum Collection, University of Texas, Austin, Tx., U.S.A.; J. Reddell.
UAIC	University of Arizona Insect Collection, Tuscon, Ariz., U.S.A.; F.G. Werner.
UFPB	Universidade Federal do Paraná, Curitiba, Paraná, Brasil; D. Urban.
UICM	University of Idaho, Department of Entomology, Moscow, Idaho, U.S.A.; W.F. Barr.
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.; T.J. Spilman.
UTDZ	University of Texas, Department of Zoology, Austin, Tx., U.S.A.; J. Rawlings.

No fossil silphids are known from Latin America. Churcher (1966) tentatively reported silphids among the insects found in the Talara late Pleistocene tar seeps of Peru. We examined these fossils, deposited in the Royal Ontario Museum, Toronto, Ontario, Canada, and found that they belong to other beetle families.

SYSTEMATICS

Key to Adults of Latin American Genera

1	Antenna clavate, the antennomeres gradually widening into an apical club (fig. 1); fronto-clypeal suture absent (fig. 3); abdominal tergum V lacking mid-dorsal stridulatory files: subfamily Silphinae	2
1'	Antenna with the apical four antennomeres forming an abrupt club (fig. 2); fronto-clypeal suture present (fig. 4); abdominal tergum V bearing a pair of mid-dorsal stridulatory files (hidden in many specimens by apices of truncate elytra): subfamily Nicrophorinae	
 <i>Nicrophorus</i> Fabricius, p. 265	
2	(1) Elytra with at least some reddish markings (fig. 5); pronotal postcoxal lobe short and broadly rounded (fig. 6)	
 <i>Necrodes</i> Leach, p. 253	
2'	Elytra wholly black; pronotal postcoxal lobe large, prominent (fig. 7)	3
3	(2') Elytra with ramose or branching sculpturing (fig. 9)	
 <i>Heterosilpha</i> Portevin, p. 253	
3'	Elytra lacking ramose or branching sculpturing	4
4	(3') Pronotum with two or four pairs of low, broad longitudinal costae on disc (fig. 1); widest at or before middle, lacking hairs on dorsal surface	
 <i>Oxelytrum</i> Gistel, p. 257	
4'	Pronotum lacking costae; widest behind middle, bearing at least some hairs on dorsal surface	5
5	(4') Head with a short row of long, erect hairs behind the eyes (fig. 11); elytra tricostate	
 <i>Oiceoptoma</i> Leach, p. 254	
5'	Head lacking a short row of erect hairs behind the eyes; elytra either lacking costae entirely (fig. 12) or with numerous tubercles on dorsal surface (figs. 13, 14).	
 <i>Thanatophilus</i> Leach, p. 255	

SUBFAMILY SILPHINAE

NECRODES LEACH 1815

Four species are known in this genus, one of which occurs in North America where it is widespread (Anderson and Peck, 1985; Ratcliffe, 1972). Adults are easily recognized by the key characters, large size and form of elytra (Fig. 5).

Necrodes surinamensis (Fabricius)

Figures 5, 6, 17

Silpha surinamensis Fabricius, 1775: 72. Type locality: "in America meridionali.". Syntypes: in Hunterian collection, University of Glasgow (Ratcliffe, 1972). Ratcliffe, 1972; Anderson and Peck, 1985.

Diagnosis.— Length 15 - 25 mm. Eyes large, separated by distance about twice width of an eye in dorsal view. Apical three antennomeres black. Pronotum black, sparsely punctate; orbicular, widest near middle (Fig. 17). Pronotal postcoxal lobe short, broadly rounded (fig. 6). Elytra tricostate, black with red markings present in apical quarter (fig. 5), some specimens also with red markings along lateral margin near midlength. Some males with hind femora greatly expanded.

Distribution.— Because *N. surinamensis* occurs in counties bordering the Rio Grande in Texas, it most likely occurs in bordering Mexico (Ratcliffe, 1972). The species name suggests that it occurs in South America. We have seen a single specimen (MCZC) labeled "Ucayale P(eru?). Maranon R., C. Sarkady" (which seemingly means where the Ucayale and Maranon Rivers meet). In the absence of any other verifiable records, and our inability to find the species in extensive collecting in Latin America, we cannot now accept the presence of the species any farther south than possibly northern Mexico.

Ratcliffe (1972) has reviewed the natural history and distribution of the species in the United States.

HETEROSILPHA PORTEVIN 1926

Two species of this endemic North American genus are known. Among Latin American silphids, they are easily recognized by the ramose or branching sculpturing on the elytra.

Key to species

- | | | |
|----|---|---|
| 1 | Males with pro- and mesotarsomeres 1-4 broadly expanded and with elytral apex not prolonged (fig. 9); females with elytral apex somewhat prolonged (fig. 8); male genitalia thicker and broader, parameres with apices thicker and down-curved (figs. 18, 19); elytra without metallic lustre |
<i>H. ramosa</i> (Say), p. 254 |
| 1' | Males with pro- and mesotarsomeres 1-4 not expanded; male and female elytral apices similar, not prolonged (fig. 10); male genitalia more thin and slender, parameres more narrow and straight (figs. 20, 21); elytra of some specimens with metallic lustre | <i>H. aenescens</i> (Casey), p. 254 |

Heterosilpha ramosa (Say)

Figures 8, 9, 18, 19; Map 1

Silpha ramosa Say, 1823: 193. Type locality: "the upper Missouri (River)". Neotype: in MCZC (designated by Miller and Peck, 1979: 93). Miller and Peck, 1979; Anderson and Peck, 1985.

Diagnosis.— Length 14 - 18 mm. Eyes small, separated by distance about four times width of an eye in dorsal view. Apical three antennomeres black. Pronotum black, uniformly and densely punctate; transverse, widest near base. Pronotal postcoxal lobe large, rounded at apex. Elytron tricostate, wholly black, with well developed branching sculpturing (fig. 9). Males with pro- and mesotarsomeres 1-4 laterally expanded, densely pubescent beneath; females with elytral apices slightly prolonged (fig. 8). Male genital characters as in key (figs. 18, 19).

Distribution.— The species is widespread throughout much of western North America (Anderson and Peck, 1985). Its natural history in Colorado is described by Brewer and Bacon (1975). Matthews (1888: 95) reports one specimen of the species from an unspecified site in northern Sonora. Horn (1894) lists it from San Pedro Martir, Baja California. We have seen the following record: Mexico. *Baja California*. Tijuana, III, 3. FMNH.

Heterosilpha aenescens (Casey)

Figures 10, 20, 21

Silpha aenescens Casey, 1886: 171. Type locality: San Francisco, California. Lectotype: in USNM (designated by Miller and Peck, 1979: 93). Miller and Peck, 1979.

Heterosilpha aenescens (Casey), Portevin, 1926: 85.

Diagnosis.— Length 14 - 18 mm. Eyes small, separated by distance of about four times width of an eye in dorsal view. Apical three antennomeres black. Pronotum black, uniformly and densely punctate; transverse, widest near base. Pronotal postcoxal lobe large, rounded at apex. Elytron tricostate, wholly black but many specimens with a metallic lustre, with well developed branching sculpturing. Males with pro- and mesotarsomeres 1-4 not expanded, not densely pubescent beneath; male and female with elytral apices similar, not prolonged in female. Male genital characters as in key (figs. 20, 21).

Distribution.— The species is known from southern to northern coastal California and southern Oregon (Miller and Peck, 1979), and may occur in northwestern Mexico. We have seen records from as far south as San Diego, California and suspect it occurs in northern Baja California, Mexico.

OICEOPTOMA LEACH 1815

Three species of the Holarctic genus *Oiceoptoma* are known from North America, one of which may enter extreme northeastern Mexico. Six species in this genus are known from the Palearctic region.

Oiceoptoma rugulosum (Portevin)

Figures 11, 16, 23

Silpha inaequalis rugulosa Portevin, 1903: 333. Type locality: Savannah, Georgia. Type: in MNHN?, not seen.

Diagnosis.— Length 13 - 15 mm. Head with short row of long, erect hairs behind eyes (fig. 11). Eyes small, separated by distance about four to five times width of eye in dorsal view. Apical three antennomeres black. Pronotum black, uniformly moderately densely punctate;

with few blackish hairs; transverse, widest near base. Pronotal postcoxal lobe broad, with right-angled apical point. Elytron black, tricostate; some specimens with elytral intervals with transverse rugose sculpturing. Elytral humeri each with a single tooth (fig. 16). Females with elytral apices prolonged to sharp points; males with apices broadly rounded.

Taxonomic status and distribution.— The species has usually been considered conspecific with *O. inaequale*, which is widespread in both eastern Canada and the United States (Anderson and Peck, 1985). Adults of the two taxa are separated most readily by those of *O. rugulosum* having a narrow elytral epipleuron (on the posterior half the upper oblique part is subequal to the lower vertical part, fig. 23) and by those of *O. inaequale* having a wide elytral epipleuron (on the posterior half the upper oblique part is at least twice the width of the lower vertical part, fig. 22). We know *O. rugulosum* to occur from Florida to Indiana to Texas. It is probably active in winter or spring. Portevin (1903: 333; 1926) cites the species from Mexico, which is possible, but records are not known to us, and from Guiana, which is an obvious error.

THANATOPHILUS LEACH 1815

Six species of this widespread genus are known to occur in North America. Three of these occur in Latin America, from central to Northern Mexico. Although primarily a northern cold-adapted taxon, some species of *Thanatophilus* occur in southern desert grasslands and shrublands. Other than two species which occur in the grasslands of southern Africa, members of the genus are Holarctic in distribution. Where they occur at more southerly latitudes they usually do so at higher elevations.

Key to species

- 1 Elytra abruptly truncate, lacking costae (fig. 12) *T. truncatus* (Say), p. 255
- 1' Elytra not abruptly truncate; tricostate and with tubercles interspersed between the costae (figs. 13, 14) 2
- 2 (1') Head and pronotum with abundant, long yellow-grey hairs; metasternal hairs yellow-grey; posterior margin of abdominal sternum VII of female unornamented, with marginal hairs only (fig. 24) *T. lapponicus* (Herbst), p. 256
- 2' Head and pronotum with shorter and darker hairs which do not entirely obscure the basal sculpture; metasternal hairs brown; posterior margin of abdominal sternum VII of female with numerous coarse crenulations or tooth-like projections (figs. 25a, 25b) *T. graniger* (Chevrolat), p. 256

Thanatophilus truncatus (Say)

Figure 12; Map 2

Silpha truncata Say, 1823: 193. Type locality: eastern Colorado. Neotype: in MCZC (designated by Peck and Miller, 1982: 154). Matthews, 1888: 95.

Philas truncata (Say), Portevin, 1903: 331.

Diagnosis.— Length 11 - 14 mm. Eyes small, separated by distance four to five times width of eye in dorsal view. Apical three antennomeres black. Pronotum black, uniformly and densely punctate; with short appressed blackish hairs over entire surface; transverse, widest near base.

Pronotal postcoxal lobe large, rounded at apex. Mesosternal hairs black. Elytra black, lacking costae, apices in both sexes abruptly truncate (fig. 12).

Natural history and distribution.— The species occurs in arid and open habitats in the southwestern United States and extends in such habitats onto the Mexican Plateau. Adults are known to be active from June to September. We have seen 76 specimens representing the following records:

MEXICO. *Chihuahua*. Pinos Altos. Santa Clara. *Coahuila*. Canon del Fuenteno, Sierra de la Madera, VII. *Distrito Federal*. Mexico City. *Durango*. Durango. El Salto, 2450-2750m, VI, 27. 32 km E El Salto, 2450 m, IX, 2. *Pedicensa* (not located), VI, 8. *Guerrero*. Chilpancingo. *Michoacan*. Rio Balsas (Rio Mescales). Tancitaro. *Nayarit*. Jesus Maria, VII, 7. La Mesa, VII, 3. *Puebla*. Puebla. *Veracruz*. Jalapa. *Zacatecas*. 40 km W Fresnillo, 2400 m, VI, 9. BMNH, CNCI, FMNH, SBPC, USNM.

Horn (1895: 227) mentions a record from "Sierra San Lazaro", Baja California. We do not know this locality. The specimen was probably destroyed in the 1905 San Francisco earthquake and fire.

Thanatophilus lapponicus (Herbst)

Figures 13, 24; Map 2

Silpha lapponica Herbst, 1793: 209, plate 52; fig. 4. Type locality: Lappland. Type: in Berlin?, not seen. Anderson and Peck, 1985. Not the species listed by Matthews, 1888: 96.

Thanatophilus lapponicus (Herbst), Portevin, 1926: 33.

Diagnosis.— Length 10 - 14 mm. Eyes small, separated by distance of four to five times width of eye in dorsal view. Apical three antennomeres black. Pronotum black, uniformly and densely punctate; with long yellow-grey hairs variably distributed over surface; transverse, widest near base. Pronotal postcoxal lobe large, rounded at apex. Mesosternal hairs yellow-grey. Elytra shorter, black, tricostate, with numerous tubercles interspersed between costae (fig. 13). Females with elytral apices prolonged and rounded (fig. 13); males with apices rounded, but not prolonged. Female with posterior margin of abdominal sternum VII unornamented, with marginal hairs only (fig. 24).

Natural history and distribution.— The species is widespread in North America, especially at higher altitudes or latitudes (Anderson and Peck, 1985). Portevin (1926: 136) states that *T. californicus* Mannerheim, a synonym of *T. lapponicus*, is distributed from California, through Central America, and along the Andes to Bolivia. This is an error. Records of this species in Matthews (1888) refer to *T. graniger*.

A single Mexican record is known to us: MEXICO; *Baja California*. Tijuana, III, 5. FMNH.

Thanatophilus graniger (Chevrolat)

Figures 7, 14, 25a, 25b; Map 1

Oiceoptoma granigera Chevrolat, 1833: 1. Type locality: Mexico. Type: in MNHN?, not seen.

Silpha lapponica Herbst, misidentification of Matthews, 1888: 96.

Diagnosis.— Length 10 - 14 mm. Eyes small, separated by distance of four to five times width of eye in dorsal view. Apical three antennomeres black. Pronotum black, uniformly and densely punctate; with short yellow-grey hairs variably distributed over surface; transverse, widest near base. Pronotal postcoxal lobe large, rounded at apex (fig. 7). Mesosternal hairs dark brown. Elytra longer, black, tricostate, with numerous tubercles interspersed between costae (fig. 14). Females with elytral apices prolonged and rounded (fig. 14); males with apices rounded but not prolonged. Females with posterior margin of abdominal sternum VII with numerous coarse crenulations or tooth-like projections, nearly as long as marginal hairs (figs.

25a, 25b).

Taxonomic notes, natural history and distribution.— This species has usually been considered conspecific with *T. lapponicus*, however, the female abdominal character clearly separates the two as distinct taxa.

The species is known only from the higher elevations of the Transverse Volcanic Sierra of Mexico, and Cerro Potosi in northeastern Mexico. Adults were collected during February, May, June, and November.

We have seen 38 specimens representing the following records:

MEXICO. *Distrito Federal*. Mexico City. *Hidalgo*. Guerrero Mills, 5. Apan, V, 1. *Jalisco*. Sayula. Mexico. Salazar, 3000 m, IX, 6. *Morelos*. Km 50 Mexico to Cuernavaca Road, VIII, 2. *Nuevo Leon*. Galeana, Cerro Potosi, 3750 m, VI, 16. *Puebla*. Ciudad Serdan (San Andres Cholchicomula). *Vera Cruz*. Jalapa. Las Vigas. No locality, II. No data, 2. BMNH, ITMM, MCZC, MHNH, SBPC, USNM.

OXELYTRUM GISTEL 1848

Several generic and subgeneric names have been used for the species of *Oxelytrum*. We are unable to find enough characters which combine to form a consistent suite justifying recognition of more than a single genus.

Adults of this genus are easily recognized by tricostate elytra, lacking ramose sculpturing, a pronotal disc lacking hairs and bearing two or four low longitudinal costae (fig. 1), and a large pronotal postcoxal lobe. We recognize eight species in the genus, most of which are confined to South America. Only the very widespread *O. discicolle* enters extreme southern Texas.

Key to species

- 1 Eyes small, not prominently protruding, separated by distance distinctly greater than three times width of an eye in dorsal view (figs. 26a, 26b) 2
- 1' Eyes large, prominently protruding, separated by distance about three times or less than width of an eye in dorsal view (figs. 1, 3) 4
- 2 (1) Pronotum with quadrangular reddish spot in posterolateral corner; pronotum and elytra with vague blue-green iridescence *O. biguttatum* (Philippi), p. 258
- 2' Pronotum wholly black; pronotum and elytra lacking trace of iridescence 3
- 3 (2') Apical three antennomeres orange-yellow *O. apicale* (Brullé), p. 258
- 3' Antenna black *O. anticola* (Guérin-Méneville), p. 259
- 4 (1') Pronotum and elytra concolorous chestnut brown to black; apical antennomere orange *O. lineatocolle* (Laporte), p. 260
- 4' Pronotum with margins orange-yellow, disc mostly or partly blackish (fig. 1); antennae various in color 5
- 5 (4') Elytral humeri rounded (fig. 27); pronotum with costae distinctly elevated 6
- 5' Elytral humeri toothed (fig. 28); pronotum with costae present but indistinct 7
- 6 (5) Apical antennomere orange-yellow; elytra with apices emarginate, sutural angles sharp (fig. 32) *O. emarginatum* (Portevin), p. 260
- 6' Apical antennomere black; elytra with apices not emarginate, the sutural angles evenly rounded or only slightly prolonged *O. erythrurum* (Blanchard), p. 261

- 7 (5') Pronotum with postcoxal lobe wholly orange-yellow; pronotum with dark coloration confined to very middle of disc; elytral apices produced and blunt (Figs. 35, 36) *O. cayennese* (Stürm), p. 262
- 7' Pronotum with postcoxal lobe wholly black; pronotum with dark coloration more extensive (fig. 1); elytral apices sharply pointed (figs. 37, 38) *O. discicollae* (Brullé), p. 263

Oxelytrum biguttatum (Philippi), NEW COMBINATION

Figures 26b, 29; Map 3

Necrodes biguttatus Philippi, 1859: 664. Type locality: Chile. Type in: MNSC; syntypes no. 2219-2220, not seen.

Silpha biguttula Fairmaire and Germain, 1859: 350. Type locality: Straits of Magellan. Type in: MNHN?, not seen.

Necrodes biguttulus (Fairmaire and Germain), Fairmaire, 1888: 27.

Hyponecrodus biguttatus (Philippi), Berg, 1901: 327. Schouteden, 1905: 199.

Paranecrodes biguttatus (Philippi), Portevin, 1921: 81. 1926: 131.

Silpha (*Paranecrodes*) *biguttata* (Philippi), Hatch, 1928: 116.

Diagnosis.—Length 12 – 19 mm. Head with eyes not prominent, separated by distance five times width of an eye in dorsal view (fig. 26b); frontal depressions absent; occipital-frontal crest acute. Antennae black. Pronotum black with vague blue-green iridescence, with quadrangular reddish spot in each posterolateral corner; transverse, about 0.6 times as long as wide; posterior angles obtusely angulate; margins not reflexed upwards; pronotal costae present but effaced. Pronotal postcoxal lobe black. Elytra black with blue-green iridescence, elytral humeri not toothed. Abdomen of both sexes with segment VII and apical portion of segment VIII orange-red, otherwise black. Males with elytral apices abruptly rounded (fig. 29); in females, slightly more prolonged and evenly rounded.

Natural history and distribution.—The species occurs in forests and open habitats in the southern half of Chile and adjacent Argentina. Adults were collected from October to April. We have seen 59 specimens representing the following records:

ARGENTINA. *Chubut*. No data, 1. No locality, XI. *Neuquen*. Nahuel Huapi, 2. Neuquen, III, IV, 4. Pucara, Parque Nacional Lanin, XII, 2. *Rio Negro*. Bariloche. Gutierrez, XI. *Santa Cruz*. Lago Argentino. Lago Blanco. Valle Tunel (not located), 2. Ventisquero Moreno, Los Glaciers, I. No data, 1. *Tierra del Fuego*. Bahia San Sebastian, Cerrillos, IV. Rio Grande. Rio McClelland (not located). San Sebastian. Ushuaia, II. No Locality, I. No data, 2. BMNH, FMLC, FMNH, LPMCN, USNM.

CHILE. *Aisen*. Golfo de Penas, I, 5. Laguna San Rafael, Taitao, X, XII. Puerto Cisnes, II. *Chiloe*. Palena. *Llanquihue*. Frutillar, I. *Malleco*. 20 km E Manzanar, 1100m, XII, 12. Termas de Tolguaca, II. *Magallanes*. Dawson Island. Esperanza (not located), I. Isla Navarina, XI. Isla Riesco, Mina Elena, II. Puerto Eden, XII. Punta Arenas, II. Useless Bay. No data, 1. *Osorno*. Parque Nac. Puyehue, Antillanca Rd., 965 m, *Nothofagus* forest, XII, 3. *Valdivia*. Corral. Enco, III. AFNC, BMNH, CNCI, MCZC, MNSC, SBPC, USNM.

Oxelytrum apicale (Brullé), NEW COMBINATION

Figures 26a, 30a, 30b; Map 4

Silpha apicalis Brullé, 1840: 74, in Brullé and Blanchard, 1840. Type locality: Potosi, Bolivia. Type in: MNHN?, not seen.

Hyponecrodus apicalis (Brullé), Kraatz, 1876: 375.

Hyponecrodus (*Katanecrodus*) *apicalis* (Brullé), Portevin, 1921: 82.

Silpha (*Katanecrodus*) *apicalis* (Brullé), Hatch, 1928: 113.

Diagnosis.—Length 9 – 11 mm. Head with eyes not prominent, separated by distance about five times width of an eye in dorsal view (fig. 26a); frontal depressions moderately deep; occipital-frontal crest obtuse. Apical three antennomeres orange red. Pronotum black;

transverse, about 0.75 times as long as wide; posterior angles broadly rounded; margins not reflexed upwards; pronotal costae distinctly elevated. Pronotal postcoxal lobe black. Elytra black; middle costa of some specimens effaced at basal one third; elytral humeri not toothed. Abdomen of both sexes black except for yellow-orange segment VIII in females. Males with elytral apices abruptly rounded (fig. 30a); in females very slightly prolonged immediately lateral to sutural apex and more evenly rounded (fig. 30b).

Natural history and distribution.— The species is known to us only from high and low elevation open habitats in northwestern Argentina and adjacent Bolivia. Adults were collected from November to April. We have seen 107 specimens representing the following records:

ARGENTINA. *Catamarca*. Catamarca, II. El Manchado, 3000 m, I; 4000 m, I. El Suncho Experimental Station, II, 6. Famabulasto (not located). La Ciénaga, 3700 m, III, 2. Las Mansas (not located), III. Los Angeles, II. Nevados del Aconquija, Quebrada de los Cazadores, 4500 m, XI; between Ingeho and Puesto de los Ojos (not located), II. Santa María Puesto de los Ojos (not located), II, 5. *Cordoba*. Cordoba, 4. Pampa de Achala, II. *Jujuy*. Abra Pampa, III. *La Rioja*. Velasco, II. Mina da Esperanza (not located), II, 5. *Tucuman*. Amaicha, 2000 m, II; Quebrada Amaicha, IX. Between El Nagalar and Santa María, III. Infiernillo, XI, 12; XII, 33; Quebrada Honda, 3400 m. San José, 2500 m, IV, 2. Siambon, III. Tafi del Valle, II, 3; III, 2; XI, 8; no date, 7. Tafi Viejo, II. Trancas, San Pedro Colalao, II. No locality, 3. FMLC, GMNH, LPMCN, MZUSP.

BOLIVIA. Pongo de Quime, VI. USNM.

Oxelytrum anticola Guérin-Ménéville), NEW COMBINATION

Figure 31; Map 5

Silpha anticola Guérin-Ménéville, 1855: 592. Type locality: Ecuador. Type in: Brussels Museum?, not seen.

Hyponecrotodes anticola (Guérin-Ménéville), Kraatz, 1876: 375.

Silpha microps Sharp, 1891: 40. NEW SYNONYMY. Type locality: Quito, Ecuador, 2895 m (9500 feet). Type in BMNH, seen.

Hyponecrotodes (Katanecrotodes) andicola (Guérin-Ménéville), Portevin, 1921: 82.

Silpha (Katanecrotodes) anticola (Guérin-Ménéville), Hatch, 1928: 114.

Silpha (Katanecrotodes) microps (Sharp), Hatch, 1928: 114.

Diagnosis.— Length 9 – 11 mm. Head with eyes not prominent, separated by distance about five times width of an eye in dorsal view; frontal depressions moderately deep; occipital-frontal crest obtuse. Antennae black. Pronotum black; transverse, about 0.75 times as long as wide; posterior angles broadly rounded; margins not reflexed upwards; pronotal costae distinctly elevated. Pronotal postcoxal lobe black. Elytra black; middle costa of some specimens effaced at basal one-third; elytral humeri not toothed. Abdomen of both sexes black except for yellow-orange segment VIII in females. Males with elytral apices abruptly rounded (fig. 31); female apices very slightly prolonged immediately lateral to sutural apex and more evenly rounded.

Notes about synonymy.— *Silpha microps* Sharp is placed in synonymy with *O. anticola* because we find no features on the type which separate it from the description or specimens of *Oxelytrum anticola* from the same general locality.

Natural history and distribution.— The species is known mostly from high elevation open habitats in the Andean countries of Ecuador, Peru, and Bolivia. Portevin (1926) cites the species from Colombia, which is possible, but we know of no records. Adults were collected during the months of December through April and in July. We have seen 17 specimens representing the following records:

BOLIVIA. La Paz, II; El Alto, 4100 m, XII; no date, 2. Oruro, 3700 m. BMNH, USNM.

ECUADOR. Latacunga, I. Machachi, VII. Quito (at Miami in aircraft, quarantine intercept), VII. 16 km N. Quito. Mitad del Mundo, III. PURC, USNM.

PERU. Cajace, 2650 m, IV. Carumas, 2200 m, IV. Chiquata, near Arequipa, 3100 m, II. Hlancayo (not located), III. Ototo (not located), 4000 m. Tacana Libra (Totora) (not located), 2. BMNH, FMLC, FMNH, LPMCN, MCZC, USNM.

Oxelytrum lineatocolle (Laporte)

Figures 33, 34; Map 6

Silpha lineatocollis Laporte, (Comte de Castelnau) 1840: 5. Type locality: Chile. Type in: MNHN?, not seen. Fairmaire and Germain, 1859: 350.

Necrodes gayi Solier, 1849: 359. Type locality: Chile. Type in: MNHN?, not seen.

Hyponecrodes lineatocollis (Laporte), Kraatz, 1876: 375.

Hyponecrodes lineaticollis (Laporte), Berg, 1901: 329.

Hyponecrodes (*Hyponecrodes*) *lineatocollis* (Laporte), Portevin, 1921: 84.

Silpha (*Oxelytrum*) *lineaticollis* (Laporte), Hatch, 1928: 115.

Diagnosis.—Length 15 – 22 mm. Head with eyes prominent, separated by distance about twice width of an eye in dorsal view; frontal depressions present but shallow; occipital-frontal crest acute. Antennae black. Pronotum wholly black to dark brown; transverse, about 0.65 times as long as wide; posterior angles obtusely angulate; margins not or else very slightly reflexed upwards; pronotal costae elevated. Pronotal postcoxal lobe black. Elytra black to dark brown; costae continuous throughout; elytral humeri not toothed. Abdomen of both sexes black except for yellow-orange anterior portion of segment VIII. Males with elytral apices abruptly rounded (fig. 33); apices in female slightly more prolonged and more evenly rounded (fig. 34).

Natural history and distribution.—The species is known from central Chile and adjacent Argentina. Adults have been collected from October to July, and are associated with both open and forested habitats. We have seen 358 specimens representing the following records:

ARGENTINA. *Neuquen*. Pampa Central, III. *Patagonia*. No other data. "NW Patagonia," 300-900 m. *Rio Negro*. El Bolson, III. BMNH, LPMCN, LACM.

CHILE. *Arauco*. Caramavida, X. Cordillera Nahuelbuta, XII, 4. *Cautin*. Bellavista, Lago Villarrica, 310 m, Valdivian rainforest, XII, 13. 3 km NE Tolten, 3 m, II, 4. Volcan Villarrica, *Nothofagus* forest, 1120 m, XII, 23; 1250 m, XII, 4. *Chiloe*. Chiloe Island. *Concepcion*. Ejido Pinares, XII. Concepcion, III, 3; IV; V, 4. 6 km S San Pedro, 360 m, *Pinus* forest, XII, 101. *Curico*. El Coigo, III. *Llanquihue*. Chamiza, III. Lago Chapo, 11.7 km E Correntoso, 320 m, Valdivian rainforest, XII, 58; 13.5 km e Correntoso, 310 m, Valdivian rainforest, XII, 24. Maullin, I. Petrohue, 600 m, I, 2. *Malleco*. Malalcahuello, 6.5 km E, 1080 m, *Nothofagus* forest, XII, 8; 14 km E, 1570 m, forest, XII. Manzanar, 1100 m, XII, 15 km W Victoria, 200 m, XII, 2. *Maule*. No locality, 1. El Pantanillo, 17 km SE Constitucion, 250 m, XI. *Nuble*. Alto Trequalemu, 500 m, 20 km SE Chovelien, I; XII, 3. Las Trancas, 1400 m, 70 km E Chillan, XII. Termas de Chillan, I. 3 km NE Tolten, 3 m, II, 4. 17.5 km S Curanipe, 50 m, I, 2. *Osorno*. Parque Nacional Puyehue, 600 m, Aguas Calientes, II, 9; Antillanca Rd., 720 m, *Nothofagus* forest, XII, 3; 4.1 km NE Anticura, 430 m, Valdivian rainforest, XII, 16. 15 km W Termas de Puyehue, Rancho Mirado, 205 m, II. 7.7 km NE Termas de Puyehue, 200 m, Valdivian rainforest, XII, 206. No locality, 6. *Santiago*. Leyda, VI. Santiago. *Tarapaca*. Mocha (doubtful record). *Valdivia*. 4.1 km W Anticura, 270 m, Valdivian rainforest, XII, 44. Enco, 120 m, III. Valdivia, X, 5; XII; no date, 5. *Valparaiso*. Quillota, VII, 2. Valparaiso, 6. AFNC, BMNH, CMNH, CNCI, FMNH, GMNH, LPMCN, MNSL, MZUSP, SBPC, USNM.

Oxelytrum emarginatum (Portevin)

Figure 3; Map 7

Hyponecrodes emarginatus Portevin, 1920b: 506. Type locality: Brazil. Type in: MNHN, seen.

Hyponecrodes (*Hyponecrodes*) *emarginatus* Portevin, Portevin, 1921: 83.

Silpha (*Oxelytrum*) *emarginata* (Portevin), Hatch, 1928: 114.

Diagnosis.—Length 14 – 18 mm. Head with eyes prominent, separated by a distance of about three times the width of an eye in dorsal view; frontal depressions present, shallow; occipital-frontal crest acute. Apical antennomere orange. Pronotum with margins orange-red, disc black; transverse, from 0.60-0.65 times as long as wide; posterior angles obtusely angulate; margins reflexed upwards in most specimens; pronotal costae elevated. Pronotal postcoxal lobe black. Elytra black; inner two costae effaced near base, middle costa effaced at basal one-third in some specimens; elytral humeri not toothed. Abdomen of males and females with segment IX and apical portion of segment VIII orange-red. Males and females with elytral hind angles abruptly rounded, apex emarginate, the sutural apices prolonged to needle-like points (fig. 32).

Variation.— One female from the Boraceia Biology Station, Salesopolis, Brazil, (MZUSP), has distinctly emarginate elytral apices but only a vaguely orange-red apical antennal segment.

Natural history and distribution.— The species is known to us only from the coastal ranges and highlands of southeastern Brazil. We have seen 11 specimens representing the following records:

BRAZIL. *Minas Gerais*. Sapucaí-Mirim, Cidade Azul, 1400 m. Virginia, Faz Campos, 1500 m. *Rio de Janeiro*. Itatiaia. Rio de Janeiro. *São Paulo*. Boraceia, 850 m, X, 3; XI. Pindamonhangaba. Salesopolis, VI. Viradouro. CNCI, MNHN, MZUSP, USNM.

Oxelytrum erythrurum (Blanchard)

Map 7

Silpha erythrura Blanchard, 1840: 75, in Brullé and Blanchard, 1840. Type Locality: Montevideo, Uruguay. Type in: MNHN, seen.

Hyponecrotodes erythrurus (Blanchard), Kraatz, 1876: 376.

Hyponecrotodes erythrura (Blanchard), Berg, 1901: 328.

Hyponecrotodes (*Hyponecrotodes*) *erythrurus* (Blanchard), Portevin, 1921: 85.

Hyponecrotodes erythrurus var. *melanurus* Portevin, 1926: 129. Type locality: not given. Type in: MNHN?, not seen.

Hyponecrotodes (*Hyponecrotodes*) *erythrurus* var. *pygialis* Portevin, 1921: 83. Type locality: not given. Type in: MNHN?, not seen.

Hyponecrotodes (*Hyponecrotodes*) *erythrurus* var. *melancholicus* Portevin, 1921: 83. Type locality: not given. Type in: MNHN?, not seen.

Silpha (*Oxelytrum*) *erythrura* (Blanchard), Hatch, 1928: 114.

Hyponecrotodes (*Hyponecrotodes*) *opacus* Portevin, 1921: 83. NEW SYNONYMY. Type locality: Bolivia. Type in: MNHN, seen.

Hyponecrotodes (*Hyponecrotodes*) *opacus* var. *tristis* Portevin, 1921: 83. Type locality: not given. Type in: MNHN?, not seen.

Silpha (*Oxelytrum*) *opaca* (Portevin), Hatch, 1928: 114.

Diagnosis.— Length 10 – 19 mm. Head with eyes prominent, separated by distance about three times width of an eye in dorsal view; frontal depressions present, shallow; occipital-frontal crest acute. Antennae black. Pronotum with margins orange-red, disc black; transverse, about 0.65 times as long as wide; posterior angles obtusely angulate; margins slightly to strongly relexed upwards in some specimens; pronotal costae elevated. Pronotal postcoxal lobe black. Elytra black; inner two costae effaced at very bases, otherwise strongly raised and glabrous; elytral humeri not toothed. Males with abdominal tergum VIII and IX with basal portion orange-red to varying degree; abdominal sternum VIII entirely black. Females with abdominal segment VIII entirely yellow-orange. Elytral apices broadly and evenly rounded in male; slightly prolonged immediately laterally of sutural apices in female. Some males with posteriorly directed lateral expansions of sternite of abdominal segments V and VI, but not appearing as prominent spines as in *O. cayennensis*.

Variation and Synonymy.— The amount of orange coloration on abdominal tergum IX (in males) varies. Portevin used this in establishing varieties. We also find coloration to be related to sex of the specimens, and cannot find any coherent pattern of geographic variation. There is also individual variation in the extent to which elytral costae are effaced. This was the main character used to define *Hyponecrotodes opacus* Portevin. Portevin (1921) described the species from only five specimens, supposedly from Brazil and Bolivia. Of these, we have seen only the type, a female. The only distinctive feature we see in it is that it has the second elytral costa completely effaced in the anterior half. It bears the following labels: a square hand written label "Bolvie / Standiger", a square machine printed label "Museum Paris / Coll. A. Grouvelle 1915", a square machine printed label in red type "TYPE", and an apparently recent square label "H. opacus Port". One specimen, labelled *O. opacus*, in the BMNH has narrower first elytral costae in the basal one third than does *O. erythrurum*. Specimens of *O. erythrurum*

from NW Argentina tend to have the second elytral costa more effaced. We conclude that the type of *O. opacum* is within the range of variation we have seen in *O. erythrurum*, and since we know of no other characters to separate it, consider the two names synonyms.

Natural history and distribution.— This species is widespread and apparently common in northern Argentina, Bolivia, southern Brazil, Paraguay, southeastern Peru, and Uruguay. It seemingly occurs in open and forested habitats. Adults have been collected in all months of the southern summer. We have seen 230 specimens representing the following records:

ARGENTINA. *Buenos Aires*. Ajo. Bahia Blanca, XI. Buenos Aires, I, 2; VI, 3; XI; no date, 3. Lago de Gomez, Junin, XII. Lago Monte, San Miguel del Monte, XII. Las Flores, Ciudad, X. La Plata, 23. Palermo, II; III, 4. Punta Lara, X. Rincon de Ajo, 5. San Fernando, XI, 8. Tiore (not located), II. Vitel, N of Chascomus, XI. *Catamarca*. Andalata. El Manchado, 3000 m, I. El Rodeo, I. Los Hoyos Mesaga (not located), 1700 m, IV, 3. *Cordoba*. Alta Gracia, XI. *Cordoba*. *Corrientes*. Corrientes, VII. *Entre Rios*. Gualaquay. Primero de Mayo, X. *Jujuy*. Digue la Cienaga, III (not located). Estero Uyto, II, 2. Sunchal, IX. *Misiones*. Iquazu, X, 3. No data, I. *Salta*. Capital, II. Coronel Moldes, II, 20. El Corralito, 15 km S Campo Quijano, II, 9. Rio Blanco, Campo Quijano, I, 11. Rosario de Lerma, II, 7. San Antonio, XI. San Lorenzo, I; XI. *Santa Fe*. Rosario, 4. Santa Fe, 3. *Tucuman*. Aguadita (not located), I, 5. Guabatal (not located), I, 2. Infiernillo, III, 6. La Higuera, IV. Parque Aconguija, XII, 2. Rio Los Sosa, 900 m, III, 2. San Pedro de Colalao, I, 3. Siambon, II, 3; III, 6; VII, 2; XII. Tacanas, I, 2; II; XII, 2. Tafi del Valle, II; XI, 16. Tafi, Taficillo, 1500 m, XI. Tucuman, Ciudad Universitaria, II; 11. Tucuman, II, 2. BMNH, CASC, FMLC, FMNH, FSCA, GMNH, LPMCN, MZUSP, SBPC, USNM.

BOLIVIA. La Paz, II. USNM.

BRAZIL. *Mato Grosso*. Maracaju. *Parana*. Curitiba, 900 m, XI. Serrinha Parana, XII, 4. *Rio Grande do Sul*. Pelotas, X; XII, 2. Rio Grande. *Santa Catarina*. No data. *São Paulo*. Sao Paulo, 2. BMNH, CMNH, MCZC, MZUSP, USNM.

PARAGUAY. *Caaguazu*. Paso Yobai (not located), X. *Cordillera*. Caacupe, X, Blacklight. FMLC, RDCC.

PERU. *Junin*. Valle Chanchamayo, 1400 m, IV. FMLC.

URUGUAY. Las Piedras, Canelones, II. Maldonado. Montevideo, II; XI; XII, 2; no date, 2. BMNH, FSCA, GMNH, USNM.

Oxelytrum cayennense (Stürm)

Figures 28, 35, 36; Map 8

Silpha cayennensis Stürm, 1826: 61. Type locality: Cayenne, French Guiana. Type in: Munich?, not seen.

Hyponecrotus cayennensis (Stürm), Kraatz, 1876: 375.

Hyponecrotus (*Hyponecrotus*) *cayennensis* (Stürm), Portevin, 1921: 85.

Oxelytrum occidentale Gistel, 1848: 190. Type locality: Brazil. Type in: probably lost.

Oxelytrum aequinoctiale Gistel, 1848: 190. Type locality: Brazil. Type in: probably lost. Madge, 1980: 357.

Silpha (*Oxelytrum*) *cayennensis* (Stürm), Hatch, 1928: 115.

Diagnosis.— Length 13 – 19 mm. Head with eyes prominent, separated by distance about two times width of an eye in dorsal view; frontal depressions present, shallow; occipital-frontal crest acute. Antennae black. Pronotum with margins and most of disc orange-red or yellow, only very middle of disc black; transverse, about 0.6 - 0.65 times as long as wide; posterior angles obtusely angulate; margins not reflexed upwards; pronotal costae present but effaced; pronotal postcoxal lobe entirely orange yellow. Elytra black; inner two elytral costae partially to almost completely effaced from midlength to basal one-third in most specimens, otherwise elevated; elytral humeri each with a single tooth (fig. 28). Males and females with abdominal segment VIII entirely orange-red; abdominal segment VII either black or with orange-red area at middle of apical margin. Males with elytral apices obliquely truncate, sutural angle evenly rounded (fig. 35); apices in female prolonged and sinuate but not sharply pointed (fig. 36). Some males with prominent posteriorly directed lateral expansions of abdominal sternites V and VI which appear as large spines.

Variation.— Specimens vary in extent of orange color on abdominal segment VII and VIII. This was used by Portevin to establish several aberrations. There is also variation in the extent to which the elytral costae are effaced. We have not been able to observe a geographic pattern

in this variation.

Natural history and distribution.— The species occurs over much of northern and central South America. It is most frequently collected in lower to middle elevation rain forest habitats and is active in all months. We have seen 268 specimens representing the following records:

BOLIVIA. *Beni*. Ivon, II. Rosario, Lago Rogagua, X. *Santa Cruz*. Buena Vista, Ichilo, II, 3; XII: no date, 2. Rio Japacani, Santa Cruz de la Sierra, 450 m, 34. CASC, CMNH, MZUSP, USNM.

BRAZIL. *Amapa*. Rio Amapani, VII. Rio Amapai, VIII, 2. Rio Branco, Boa Vista, I. Serra do Navio, X, 5. *Amazonas*. Manaus, INPA Station, VII; X. Maues, II, 3. Reserva Ducke, 26 km ex Manaus, I; III; V, 45. Rio Purus, Hyutanaha. *Mato Grosso*. Reserva Humboldt, Bento Mascarenhas (not located). Serra do Norte (not located), III. Xavantina, gallery forest. *Minas Gerais*. Bello Horizonte, IV. Miscosa (not located), XI. *Para*. Cachimbo. *Rio de Janeiro*. Rio de Janeiro. *Rondonia*. V. Rondonia, 378 km S P. Velho, 387 km S P. Velho, I. *São Paulo*. Boraceia, Casa Grande, I, 2. USNM, SBP, INPA, MZUSP, MCZC, UFPB.

COLOMBIA. *Amazonas*. Leticia, rainforest, II. *Cundinamarca*. Bogota, no date, 4. *Norte de Santander*. 35 km S Cucuta, Quebrada Honda, 700 m, V, 4. SBPC, USNM.

ECUADOR. *Manabi*. 78 km NE Chone, 450 m, VI, 2. *Napo*. 12 km SW Tena, 500 m, VII, 21. *Pastaza*. Puyo, II, 8. 22 km SW Puyo, 900 m, VII, 5; 22 km W Puyo, II. *Pichincha*. Rio Palenque Station, 47 km S Santo Domingo, rainforest, V, 7. Tinalandia, 16 km SE Santo Domingo, lower montane rainforest 680 m, II, 2; VI, 61. SBPC, USNM.

FRENCH GUIANA. Marioni River, Duserre. Mana River, V. CMNH, USNM.

GUYANA. Bartica. Essequibo River, Morabaldi Creek; Monkey Jump. Kartabo, VIII, 2. Membaro Creek, upper Mazaruni River. Oronoque and New River Heads. BMNH, FMNH, MCZC.

PERU. *Loreto*. Estiron, Rio Ampiyachu, XI, 2. *Junin*. La Merced. Valle Chanchamayo, 800 m, I, 2. BMNH, FMLC, FMNH.

VENEZUELA. *Amazonas*. Mt. Marahuaca, N slopes, V, 9. Paraitepuy, 4. *Aragua*. Rancho Grande, N of Maracay, VI. *Zulia*. Kunana, Perija, 1100 m, Rio Negro, XII, 8. IZAV, USNM.

Oxelytrum discicollis (Brullé)

Figures 1, 3, 15, 37, 38; Map 9

Silpha discicollis Brullé, 1840: 75, in Brullé and Blanchard, 1840. Type locality: Altamachi River, near Cochabamba, Bolivia. Type in: MNHN?, not seen.

Hyponecros discicollis (Brullé), Portevin, 1905: 50.

Hyponecros (*Hyponecros*) *discicollis* (Brullé), Portevin, 1921: 85.

Silpha (*Oxelytrum*) *discicollis* (Brullé), Hatch, 1928: 115.

Necros analis Chevrolat, 1843: 26. Type locality: Orizaba, Mexico. Type in: MNHN?, not seen.

Hyponecros analis (Chevrolat), Kraatz, 1876: 376. Matthews, 1888: 95.

Hyponecros (*Hyponecros*) *discicollis* var. *elongatus* Portevin, 1921: 84. Type locality: not given. Type in: MNHN?, not seen.

Hyponecros (*Hyponecros*) *discicollis* var. *discretus* Portevin, 1921: 84. Type locality: not given. Type in: MNHN?, not seen.

Silpha (*Oxelytrum*) *discicollis* (Brullé), Hatch, 1928: 115.

Diagnosis.— Length 11 – 19 mm. Head with eyes prominent, separated by distance about twice width of an eye in dorsal view (fig. 3); frontal depressions shallow; occipital-frontal crest acute. Antennae black. Pronotum with margins orange-red, disc black; transverse, about 0.6-0.65 times as long as wide; posterior angles obtusely angulate; margins very slightly reflexed upwards in some specimens; pronotal costae present but indistinct. Pronotal postcoxal lobe black. Elytra black; inner two costae effaced at base in most specimens; middle costa partially to completely effaced from midlength to basal one-third in most specimens, otherwise costae elevated; elytral humeri each with a single tooth (fig. 15). Males and females with abdominal segment VIII entirely orange; tergum of abdominal segment VII with orange-red spot of variable size at apical margin, otherwise black. Males with elytral hind angles evenly rounded, sutural angles very slightly prolonged to a sharp point (fig. 37); apices in females slightly prolonged and with sutural spines very slightly longer than in males (fig. 38). Some larger males with lateral margins of abdominal sterna V and VI very slightly produced laterally.

Variation.— The extent of the orange coloration of abdominal segment VII varies within and between sexes of a single population. This variation was used by Portevin to establish aberrations. There is also variation in the extent to which the elytral costae are effaced.

Natural history and distribution.— This is the most commonly collected species of silphid in Latin America. Many adults are attracted to carrion baits, and come commonly at night to ultraviolet and other light traps. The species is distributed from southern Brazil and Paraguay, through much of central and northern South America (but not the lowlands of the Amazon Basin), through Central America, to Mexico and extreme south Texas. Adults have been collected in every month of the year, in habitats ranging from rainforest to montane cloud forest from near sea level to more than 3000 m elevation, and in open semi-arid thorn-scrub vegetation. We have seen 3096 specimens representing the following records:

ARGENTINA. *Misiones*. Cataracas de Iguazu, XI. Eldorado, XI, 2. Iguazu, III, X. FMLC, USNM.

BELIZE. Belmopan, 50 m, rainforest, VIII, 2. 6 km S. Belmopan, VIII, rainforest. SBPC.

BOLIVIA. *Cochabamba*. Alto Palmar, 800 m, X. Chaparé, 1000 m. Cochabamba. Incachaca, 2500 m, 30. *La Paz*. La Paz. Yan(aca)chi (?). *Santa Cruz*. Carahuasi, 250 km E Cochabamba, 3000 m, VII. Santa Cruz, 300 m. Parapeti, X, 4. Yanchi. CMNH, FMLC, MZUSP, USNM.

BRAZIL. *Amazonas*. Tucano, 1500 m, IV, 2. *Bahia*. Salvador, VIII. *Distrito Federal*. Brasília. Foresta da Tijuca, VIII. *Espirito Santo*. No data. Guarapari, 3. *Minas Gerais*. Bello Horizonte, IV. Lambari, XI. Laveras, III. Vicosia, III. Serra do Caraca, XI, 13; XII, 8. Sapucaí-mirim, Cda. de Azul, 1400 m, XI, 2. *Parana*. Banhados (Curitiba to Paranaguá), 800 m, II, 34. Foz do Iguazu, IX, 2; XII, 4. Guaixa (not located), XII. Jaguariáiva, I. Marumbi, II, VI. Quatro Barras, III, 3. São João, Guayra. S. J. Pinhais (not located), I, 3. *Rio de Janeiro*. Angra dos Reis, IX, 6. Rio de Janeiro, X; no date, 3. Itatiaia, II, 3. Ouro Preto. Petropolis, Km 50 Estrada Contorno, 900 m, XI. Teresopolis, XII. *Rio Grande do Sul*. Cochoeira (not located), X. *Santa Catarina*. Nova Teutonia, III, 4; no date, 11. Rio dos Autos Camayo, I. Rio dos Reis, 3. *São Paulo*. Alto da Serra, IX; 3. Anbemi (not located), 7. Barreiro, Serra do Bocaira, II. Bariero (not located), III. Barueri, I; II; III; VI; XI, 4; XII, 3. Boraceia Station, Salesopolis, 850 m, I, 2; II, 2; III; IV, 4; XII, 2; no date, 14. Campos de Jordao, 13, no date; XI. Jaba-quara, X. Consobacao (not located), II. Faz Campinas, Mogi Guacu, I, 13. Mogi das Cruzes. Iguap, 2. Jpiranga, XI. Pampeia (not located), VIII. Parana Macaba, III. Pindamonhangaba, I, 16; III; IX, X, 9. Porto Cabral, X. Paranapicaba. Piracicaba, XII, 9. S. Bernardo, 2. Santana, II, 6; VI; X; XI; XII, 4. San Jose dos Campos, IX. Opatco, I. São Paulo, 3. Tremembe, III. Ypiranaga, XI; XII, 2. CNCI, FSCA, GMNH, IZAV, MZUSP, UFPB, USNM.

COLOMBIA. Cundinamarca. Bogota, 6. Cajica, I. Sasaima, IV. *Cesar*. Valledupar, 1300 m, 2. *Guajira*. Sierra de Perija, Socorro Mission, 1400 m, IX, 5. *Magdalena*. Campana, 26 km S Santa Marta, 1050 m, V. El Libano, 1800 m. *Meta*. E of Villavicencio, no date. 23 km NW Villavicencio, Quebrada Suumuco, 1000 m, III, 3. *Narino*. Mallama. *Norte de Santander*. 2 mi N Chinacota, 900 m, V. 32 km S Cucuta, Quebrada Honda, 600 m, V, 2. *Putumayo*. Santa Rosa, Rio San Miguel. *Quindio*. No data. *Valle*. Km 18 Buenaventura Hwy, I. BMNH, CASC, CMNH, FMNH, FSCA, SBPC, USNM.

COSTA RICA. *Alajuela*. Poasito, Volcan Poas, 1840 m, VII, 14. *Cartago*. Irazu, 1650 m, II; 2200 m, II; 3000 m, IX, 2. Turrialba, III, 2; VIII, 2; IX, 2. *Puntarenas*. Coronado, VI; VII, 4. La Palma (1500 m?), VI. Monteverde, 1400 m, V, 4; VI, 4; VII, 2; 1500 m, II; VI, 2. 21 km NE Potrero Grande, IX, 3. 6 km N Santa Elena, 1400 m, V. *San Jose*. Carillo. San Jose, 1172 m, VIII, 6; 1200 m, I; no date, 2. 14 km N San Isidro; 1600 m, VI. CMNH, CNCI, FSLC, LACM, SBPC.

ECUADOR. *Guayas*. Guayaquil. *Loja*, 2220 m, 7. San Ramon, 27 km WSW, V, 7. *Napo*. Baeza, 2000 m, III, 20. 6 km N Baeza, 2000 m, II, 29. 17 km NE Baeza, 4 km SW Chaco, III, 32. 7 km S Baeza, 2000 m, II, 61. 125 km NW Baeza, 2000 m, III, 2. 24 km NE Baeza, 1200 m, III, 4. *Pastaza*. 1 km E Mera, 1100 m, VII. *Pichincha*. 28 km NE Alluriquin, Chiriboga Road, 1600 m, VI, 8. 3 km E Tandapi, 1300 m, VI, 25. 18 km E Tandapi, 1800 m, VI, 24. 24 km E Tandapi, 2300 m, VI, 60. 16 km E Tandapi, 2000 m, VI, 3. *Tungurahua*. Banos, 1200 m, Mera Trail, IX; 1800 m, IX, 7. 39 km E Banos, I. 6 km E Rio Negro, 1400 m, VII. 8 km E Rio Negro, 1500 m, VII, 13. CASC, SBPC.

EL SALVADOR. 16 km N Metapan, Montecristo, 1760 m, V. SBPC.

GUATEMALA. *Alta Verapaz*. Coban, VI, 2. Patal, 5 km S Tactic, 1350 m, VIII. *Chimaltenango*. Yepocapa, VIII. *Peten*. Pacomon (not located), VI, 2. SBPC.

MEXICO. *Chiapas*. 32 km N Bochil, 1700 m, VIII, 3. Cerro Tres Picos, 2000 m, 5. 8 km SW El Bosque, VI. Montebello Lagunas, VIII. Ocozocautla, 800 m, 2. Rosario Izapa. San Cristobal de las Casas, V, 2; VIII, 5. Santa Rosa, VIII, 3. *Distrito Federal*. No data. *Durango*. 66 km SW Ciudad de Durango, 2300 m, VI, 15. *Guerrero*. 6.5 km W Miatlan, 1450 m, IX, 3. 12 km W Mayatlan, Microondas, 2150 m, IX. *Hidalgo*. 4.5 km N Tlanchinol, 1600 m, VIII, 2. *Jalisco*. 9.5 km W Atenquique, 1700 m, IX, 2. 15 km SW Autlan, 1300 m, IX, 2. 19 km SW Cocula, 1750 m, IX, 2. Los Volcanes, 1650 m, near El Rincon. *Mexico*. 5 km S Temascaltepec, 2000 m, IX, 2; 9.6 km NE, 2150 m, IX, 4. 8 km SW Tenancingo, 2200 m, IX. Valle de Bravo, 1830 m, XI, 2. *Michoacan*. Morelia. Patzcuaro, IX, 2. San Jose Purua, II. Tacambaro. Tancitaro, 1850 m, VIII, 4. Urapan, VIII. *Morelos*. Cuernavaca, I; VII. No data, 2. 12 km E Cuernavaca, VII, 2. *Nayarit*. Tepic, VII, 3. *Nuevo Leon*. Allende. 29 km W Linares, Santo Rosa Canyon, 700 m, oak-thorn forest, VI,

2. Monterrey, Chipinque Mesa, 1350 m, V; VI; VII. Monte Peila, V. 21 km W Montemorelos, Cueva de Chorros de Agua, VI, 5; Chorros de Agua, VI, 291. Rayones, III, 2. *Oaxaca*. 14.5 km E El Camaron 1300 m, IX. Juquila Mixes, 1450 m, VI; VII. Oaxaca, VI; VIII. 14.5 km NE Oaxaca, 1900 m, VII, 24. 147 km N Oaxaca, V. Sierra Madre del Sur, Escondido Road Crest, VI, 28. 24 km S Sola de Vega, 1850 m, V, 5. 13.5 km S Suchixtepec, IV. 5 km N Suchixtepec, 2900 m, VI. 12 km S Valle Nacional, 900 m, V, 18. Temascal, VI. *Peubla*. Cholula. 7 km SW Huauchinango, 1700 m, VII. Villa Juarez, X. *Queretaro*. 29 km E Landa de Matamoros, 1600 m, VI, 2. 32 km W Xilitla, 1600 m, VI, 9. *San Luis Potosi*. 24 km W El Naranjo, 1100 m, VI, 2. Cueva de la Puente, 20 km S San Francisco, 3000 m, V. *Sinaloa*. 62 km NE Concordia, 1900 m, IX. El Palmito, VII, 3; 2200 m, VIII. 7 km NE La Capilla del Taxte (not located), VI, 2. *Tamaulipas*. 7 km W El Encino, III, 6. Gomez Farias, Rancho del Cielo, cloud forest, 1000 m, 1150 m, VI; VII, 19. Sotano de las Salas, I. *Veracruz*. Catemaco, V, 2. Chocaman, VII. Cordoba, I, 2; II, 3; III; VII, 3; VIII, 3; IX, 6; XII; no date, 3. 7 km N Huatusco, 1300 m, VII; VIII, 3. Jalapa, V, 2; VI, 2; VII, 2; no date, 8. Orizaba, I; XI, 3; XII, 6. Perote, V, 2. Presidio, X. Rio Metlac, near Fortin, 1000 m, VI, 2; VII, 40. Sumidero, near Fortin, 750 m, V, 6. 22.5 km S Tlapacoyan, 120 m, VII. Cueva de Tlilapan, 5 km S Orizaba, VIII. BMNH, CASC, CNCI, FMNH, ITMM, LACM MHNH, RDCC, SBPC, TMMC, USNM, UTDZ.

NICARAGUA. Chontales. BMNH.

PANAMA. *Bocas del Toro*. 20 km SE Chiriqui Grande, 900 m, VI, 7. *Chiriqui*. Boquete, IX, UV Light, 5. Boquete, Alto Lindo, VII, 2; IX, UV light, 8. 5 km W Boquete, El Salto Road, 1610 m, VI, 3. 10 km W Cerro Pando, V, 39. 2 km W Cerro Punta, 1760 m, V, 2; VI, 159. 2 km E Cerro Punta, 2200 m, VI, 37. La Fortuna Dam, 800 m, VII, 11; 1000 m, VII, 4. 4 km W Hato del Volcan, 1360 m, VI, 301. Lagunas, 5 km SW Hato del Volcan, 1360 m, VI, 273. 2 km N Santa Clara, Hartman Finca, 1200-1500 m, V, 375; VI, 41. Volcan de Chiriqui, 1200-1900 m, 4. BMNH, GMNH, SPBC, USNM.

PARAGUAY. *Alto Parana*. Puente Stroessner, VIII, 8. *Caaguazu*. Paso Yobai (not located), X. *Itapua*. Trinidad, X. *Misiones*. Loreto, VI, 5; X, 2. No location, 2. *Paraquari*. Parque Nacional Ybycui, I, 4. *Parana*. Iguazu, X. *San Pedro*. Carumbe (not located), II. FMLC, GMNH, LPMC, RDCC.

PERU. *Cuzco*. Cuzco, VIII. Marcapata, Hacienda Cadena, VIII. *Huanuco*. N side Cerro Carpath, nr. Chinchao, 1920 m, montane rainforest, I, 2. *Junin*. Perene, 600-900 m. Valle Chanchamayo, 1400 m, I; II. *La Libertad*. Samne, 1500 m, VII. *Pasco*. Huancabamba, 3000 m, 2. *Ucayali*. Sinchono (= Fundo Chinchona), 1300 m, V. La Divisorio, 1400 m, V. AFNC, FMLC, USNM.

VENEZUELA. *Aragua*. Camp Rangel, VII. Choroní, V; Km 27, VI, 2; Km 25, III, 2; 9000 m, X, 10. Rancho Grande, N of Maracay, 1100 m, I, 2; II, 78; III, 7; IV, 4; V, 9; VI, 27; VII, 5; VIII, 26; IX, 1; X, 2; XI, 2; XII, 5; 1500 m, II, 6; 1700 m, V. *Bolivar*. El Dorado - Santa Elena, Km 107, 520 m, VIII, 10; Km 109, VIII, 3; Km 38, 160 m, VIII; Km 125, 1100 m, IX, 3. *Carabobo*. Borburato, III, 2. *Distrito Federal*. Caracas, Quebrada de Catuche, VI. Caracas. El Avila, 1400 m, X. El Junquito, 1900 m, VI, 7. El Limon, 1350 m, VI, 14. Macizo, Naiguanta, IX. *Lara*. Terapaima (not located), XI. *Merida*. Merida, 5; La Pedregosa, 1800 m, IX, 4. Mucay (not located), IX. Santa Rosa, X, 2. *Miranda*. Fila de Mariche (not located), 1200 m, III. San Antonio de los Altos, 1300 m, IV; V; VII; VIII, 28; IX, 31. *Sucre*. Carripa (not located), VI. *Tachira*. San Cristobal, 1200 m, VIII, 7. 20 km NE San Cristobal, 1200 m, V, 11. 38 km NE San Cristobal, 2150 m, V, 12. *Trujillo*. Bocano, VIII, 16. *Yaracuy*. San Felipe. CMNH, CBMV, IZAV, MZUSP, SBPC, USNM.

UNITED STATES. *Texas*. Willacy County, Lyford, VI (record in Davis, 1980). This is the only known United States record.

SUBFAMILY NICROPHORINAE

NICROPHORUS FABRICIUS 1775

These large insects are commonly called burying or sexton beetles. About 85 species are known in the genus throughout the world. Most live in Europe and Asia. In the Old World, they occur only as far south as Ethiopia in Africa and in southern Asia to New Guinea and the Solomon Islands. Fifteen species live in the United States and Canada. Nine species are known in Latin America, from Mexico southward to southern Chile and Argentina.

Key to species of *Nicrophorus* in Latin America

- | | | |
|----|--|--|
| 1 | Posterior lobe of metepimeron (fig. 39) with many long golden hairs | 2 |
| 1' | Posterior lobe of metepimeron with only a few dark hairs or glabrous | 3 |
| 2 | (1) Anterior face of procoxa with short hairs; elytral maculations large (figs. 2, 45, 48) | <i>N. marginatus</i> Fabricius, p. 266 |

- 2' Anterior face of procoxa with long hairs; elytral maculations large, reduced or absent (figs. 40-44) *N. guttula* Motschulsky, p. 267
- 3 (1') Dorsal ridge of elytral epipleuron long, extending anteriorly to or past level of apex of scutellum (fig. 46) 4
- 3' Dorsal ridge of elytral epipleuron short, not extending to level of apex of scutellum (fig. 47) 5
- 4 (3) Elytron fasciate (fig. 54b); elytral epipleuron orange-red with pre-basal black spot (fig. 54a) *N. mexicanus* Matthews, p. 267
- 4' Elytron and elytral epipleuron wholly black *N. nigrita* Mannerheim, p. 268
- 5 (3') Elytral epipleuron predominantly or wholly black 6
- 5' Elytral epipleuron from about half to predominantly or wholly orange-red 7
- 6 (5) Elytral epipleuron wholly black; dorsal surface of elytra with abundant long hairs; each elytral fascia entire, four elytral spots in total (fig. 49) *N. quadrimaculatus* Matthews, p. 268
- 6' Elytral epipleuron black with orange-red spot at base (fig. 50a); dorsal surface of elytra with few long hairs; each elytral fascia of most specimens divided into two spots, thus eight elytral and two epipleural spots in total (fig. 50b) *N. didymus* Brullé, p. 268
- 7 (5') Apical three antennomeres black; elytral epipleuron orange-red with black spot at base (fig. 51a); elytra with fasciae confluent, dorsal surface largely orange-red (fig. 51b) *N. chilensis* Philippi, p. 269
- 7' Apical three antennomeres orange-red; elytral epipleuron wholly orange-red; elytral pattern various 8
- 8 (7') Anterior and posterior elytral fasciae confluent laterally (fig. 52b); elytra with dorsal surface with abundant hairs *N. olidus* Mathews, p. 269
- 8' Anterior and posterior elytral fasciae not confluent (fig. 53b); elytra with dorsal surface with but few long hairs, most confined to lateral margins *N. scrutator* Blanchard, p. 270

Necrophorus marginatus Fabricius

Figures 2, 4, 45, 48; Map 10

Necrophorus marginatus Fabricius, 1801: 334. Type locality: "North America". Type: location unknown, not seen. Miller and Peck, 1979; Anderson and Peck, 1985.

Necrophorus montezumae Matthews, 1888: 92. Type locality: Mexico. Type in: BMNH, seen.

Diagnosis.—Length 15–22 mm. Pronotum markedly cordate, with narrow lateral margins and wide basal margin (fig. 2). Anterior face of procoxa with short black hairs. Apical four antennomeres orange-red. Metasternal pubescence dense, yellow; metepimeron with dense yellow pubescence. Hind tibiae slightly curved. Elytron with epipleural ridge long, extending to about level of base of scutellum (figs. 45, 46); dorsal surface lacking hairs; elytron with pattern as in figures 2, 45, 48.

Natural history and distribution.—The species is widespread in open grassland, old field, and shrubby habitats from southern Canada and most of the United States into northern Mexico (Anderson and Peck, 1985). Adults have been collected throughout the summer months. We have seen the following 17 records:

MEXICO. *Coahuila*. 14 km NW Saltillo, VII. Parras. Rancho Encantada, Sierra de la Encantada, VII. *Distrito Federal*. Mexico City. *Durango*. Villa Lerdo. 32 km E El Salto, 2400 m, VI, 9. *Puebla*. Cholula, Esperanza. *Veracruz*. Jalapa. BMNH, CNCI, SBPC.

Nicrophorus guttula Motschulsky

Figures 40-44; Map 10

Nicrophorus guttula Motschulsky, 1845: 53. Type locality: Sitka, Alaska. Type: in Leningrad?, not seen. Miller and Peck, 1979; Peck and Miller, 1982; Anderson and Peck, 1985

Diagnosis.—Length 14–20 mm. Pronotum markedly cordate, with narrow lateral margins and wide basal margin. Anterior face of procoxa with long black hairs. Apical three antennomeres orange-red or black. Metasternal pubescence dense, yellow; metepimeron with dense yellow pubescence. Hind tibiae slightly curved. Elytron with epipleural ridge long, extending almost to level of base of scutellum (figs. 40a, 44a). Elytral pattern various, as in figures 40-44.

Taxonomic notes and distribution.—The species is widespread in dry forests and grasslands in southwestern Canada and the western United States. The more conspicuously maculate individuals were formerly called *N. hecate* Bland (Peck and Miller, 1982). Border records indicate that the species probably occurs in northwestern Mexico. We know only of the following record:

MEXICO. *Baja California*. Valle de Trinidad, Aguajito Spring, III, 3, SDMC.

Nicrophorus mexicanus Matthews

Figures 46, 54; Map 11

Nicrophorus mexicanus Matthews, 1888: 91. Type locality: Mexico. Type in: BMNH, seen.

Diagnosis.—Length 14–18 mm. Pronotum quadrate, with wide lateral and basal margins. Apical three antennomeres orange-red. Metasternal pubescence dense, dark brown; metepimeron with small tuft of dark brown hairs. Hind tibiae straight. Elytron with epipleural ridge long, extending almost to level of base of scutellum (fig. 46); dorsal surface lacking hairs. Elytron with pattern as in figure 54.

Natural history and distribution.—The species occurs in habitats ranging from semi-arid and open thorn scrub to moist closed-canopy cloud forests in the southwestern United States, through Mexico, to Guatemala and El Salvador. Over its southern range, adults have been collected in all months of the year. Zaragoza and Pérez (1975) give a morphometric and seasonal analysis based on 436 specimens collected in black light traps over three years near Mexico City. They report *N. mexicanus* to be most abundant in October. Reproductive behavior has been studied by Halfpeter *et al.* (1982). We have seen 127 specimens representing the following records:

EL SALVADOR. Montecristo, 23 km N Metapan, 2300 m, cloud forest, V, 8. SBPC.

GUATEMALA. *Zacapa*. Jabah, S slope Sierra Minas, VII. FMNH.

MEXICO. *Chiapas*. 5 km W San Cristobal de las Casas, 2440 m, IX, 2. *Chihuahua*. Mesa del Huracan, 2557 m, VII, 4. Nuevo Casas Grandes, 20 km SE, Hwy 10, 1700 m, VIII. Sierra de la Catarina, 30 km SW Buenaventura, 2600 m, VIII, 9. Sierra de Choreachic, Microwave Sta. Hwy 16, 30 km W Cuauhtemoc, 2500 m, VIII. Sierra Huachinera, 30 km SW Colonia Juarez, 2200 m, VIII, 3. *Distrito Federal*. Lomas, V. Mexico City, V. No locality, III. *Durango*. 5 km W El Salto, 2745 m, VI, 15; VII, 8. 16 km W El Salto, 2745 m, VI; VII, 16; VIII. 66 km SW Durango, 2250 m, VI, 2. Ciudad de Durango, 1800 m, IV. 38 km W La Ciudad, VII, 20. 32 km E El Salto, 2400 m, VI, 5. 54 km E El Salto, 2100 m, IX, 5. *Guerrero*. 12 km W Mazatlan, 2130 m, IX, 3. *Hidalgo*. Guerrero Mills. 10 km S Tenango de Doria, 3000 m, VII, 5. *Mexico*. Ayolita. *Nuevo Leon*. Galeana, 2217 m. Iturbide, 1800 m, VII, 3. *Oaxaca*. La Parada. Sierra Madre del Sur, Escondida Road Crest, VI. 5 km N Suchixtepec, 2850 m, VI. Yolotepec. Road to Yuquila, 2430 m, VIII. oak-pine forest, 2. *Tamaulipas*. Gomez Farias, Rancho del Cielo, 2000 m, XII. *Tlaxcala*. 3 km S Apizaco, pine forest, VI, 3. BMNH, CNCI,

FMNH, LACM, MCZC, MHNH, OSUC, SBPC.

Necrophorus nigrita Mannerheim
Map 10

Necrophorus nigrita Mannerheim, 1843: 251. Type locality: California. Type: in Helsinki?, not seen. Miller and Peck, 1979; Anderson and Peck, 1985.

Diagnosis.— Length 13 – 18 mm. Pronotum quadrate, with wide lateral and basal margins. Apical three antennomeres orange-red. Metasternal pubescence dense, dark brown; metepimeron glabrous. Hind tibiae straight. Elytron with epipleural ridge long, extending almost to level of base of scutellum; dorsal surface lacking hairs. Elytron wholly black.

Natural history and distribution.— The species occurs in drier forests on the Pacific coast from British Columbia to southern California, including the Channel Islands (Miller and Peck, 1979). Horn (1876, 1880) lists the species from Guadalupe Island, Baja California. We know of only the following Mexican records:

MEXICO. *Baja California*. Guadalupe Island, 5 (not shown on map). 10 km E El Rosario, uv light, III. MCZC, UICM.

Necrophorus quadrimaculatus Matthews
Figures 49, 55; Map 12

Necrophorus quadrimaculatus Matthews, 1888: 93. Type locality: Guatemala. Type in: BMNH, seen.

Diagnosis.— Length 9 – 16 mm. Pronotum orbicular with wide lateral and basal margins (fig. 55). Apical three antennomeres orange-red. Metasternal pubescence moderately dense, dark brown; metepimeron with long dark brown hairs. Hind tibiae very slightly curved. Elytral epipleural ridge short (as in fig. 47); dorsal surface of elytron with long, dense hairs. Elytron with pattern as in figure 49. Metatrochanter with sharp spine.

Natural history and distribution.— The species ranges from southern Mexico to western Panama. Adults have been collected only from June to September, and only in montane pine or cloud forests. We have seen 52 specimens representing the following records:

COSTA RICA. *Puntarenas*. Monteverde, 1400 m, VI; VII, 2; IX; 1520 m, VII; 1700 m, V. No data, 2. BMNH, CMNH, LACM, SBPC.

EL SALVADOR. 16 m N Metapan, Montecristo, 1760 m, mixed pine forest, V, 2. SBPC.

GUATEMALA. *Alta Verapaz*. 6 km S Coban, 1373 m, VIII, 5. Patal, 5 km S Tactic, 1373 m, VIII. Senahu, 1098 m, VIII. *Baja Verapaz*. San Jeronimo. *Quezaltenango*. Volcan Zunil. BMNH, SBPC.

MEXICO. *Chiapas*. Lagunas de Montebello, 1373 m, VIII, 1 km SW Rizo de Oro, 834 m, VIII. SBPC.

PANAMA. *Chiriqui*. 4 km N Santa Clara, Cerro Pelota, Hartman Finca, 1200 m, V; 1500 m, V, 20; VII, 6; VIII, 5. SBPC.

Necrophorus didymus Brullé
Figure 50; Map 13

Necrophorus didymus Brullé, 1840: 73. in Brullé and Blanchard, 1840. Type locality: Altamachi River, eastern mountain slopes, Cochabamba, Bolivia. Type in: MNHN?, not seen. Berg, 1901: 326; Portevin, 1903: 331.

Necrophorus didymus var. *peruvianus* Pic, 1917: 2. Type locality: Peru. Type in: MNHN?, not seen.

Necrophorus flexuosus Portevin, 1924: 191. Type locality: not given. Type in: MNHN?, not seen. Hatch, 1928: 128.

Necrophorus flexuosus var. *portevini* Pic, 1933: 6. Type locality: Merida, Venezuela. Type in: MNHN?, not seen.

Diagnosis.— Length 13 – 16 mm. Pronotum orbicular with wide lateral and basal margins. Apical three antennomeres orange-red. Metasternal pubescence moderately dense, dark brown; metepimeron with few short brown hairs. Hind tibia very slightly curved. Elytron with epipleural ridge short, not extending to base of scutellum; dorsal surface with long and

moderately dense hairs. Metatrochanter with spine reduced or absent. Elytra with pattern as in figures 50a, 50b.

Variation.— Many elytral patterns have received varietal and aberrational names. The elytral maculations vary from two distinct bars to four distinct spots (a pair of spots forming from a color bar) on each elytron. We have not seen a pattern of geographic variation in such coloration.

Natural history and distribution.— The species occurs in middle to upper elevation Andean forests from Venezuela through Colombia, Ecuador, and Peru to Bolivia. We believe literature records for the species from Mexico, Central America, and Argentina pertain to other species. Adults have been collected during eight months of the year. We have seen 76 specimens representing the following records:

BOLIVIA. *Cochabamba*. Incachaca, 2300 m. MCNH.

COLOMBIA. *Antioquia*. Medellin. *Magdalena*. Rio Don Amo, 600 m, VII. Rio Don Diego, 36 m, VII. No other data. BMNH, CMNH.

ECUADOR. *Napo*. 7 km S Baeza, 2000 m, II, 2. El Chaco, 2000 m, II. *Province Unknown*. Mangosia River (not located), 650 m. BMNH, SBPC.

PERU. *Huanuco*. N side Cerro Carpish, near Chinchao, cloud forest, 2300 m, I, 24; 2400 m, I. *Pasco*. Oxapampa, 1800 m, I. Pozuzo (10°4'S 75°32'W). AFNC, FMLC, SBPC, USNM.

VENEZUELA. *Aragua*. Cerro Choroní, 1600 m, II. Rancho Grande, N of Maracay, 1500 m, II, 8; V; VIII, 2; XII. Maracay to Choroní, 1000 m, XII; 1300 m, XII. *Distrito Federal*. Caracas, no data. Caracas, Rio Caurimare, 1000 m, V, 7. El Junquito, VI; X. El Limon, 1350 m, VI, 5. *Lara*. Cabudare, Terepaima Creek, 1200 m, I. *Tachira*. San Cristobal, 1200 m, VIII, 17. *Trujillo*. Bocono, VIII. *Zulia*. Sierra de Peria, Kunana, 1100 m, XII. BMNH, CBMV, IZAV, SBPC.

Nicrophorus chilensis Philippi

Figure 51; Map 14

Nicrophorus chilensis Philippi, 1871: 293. Type locality: Santa Cruz, Curico, Chile. Type in: MNSC, holotype no. 171, not seen.

Diagnosis.— Length 13 – 16 mm. Pronotum subquadrate with wide lateral and basal margins. Apical three antennomeres black. Metasternal pubescence dense, dark brown; metepimeron glabrous. Hind tibiae straight. Elytron with epipleural ridge short, not extending to level of apex of scutellum; dorsal surface lacking hairs. Metatrochanter with sharp spine. Elytron with fasciae confluent and large, pattern as in fig. 51.

Variation.— The anterior and posterior elytral maculations of some specimens are joined and may be so large that the black area is reduced to only the extreme anterior and posterior sutural margins of the elytra.

Natural history and distribution.— The species apparently occurs in open and semi-arid areas of central Chile and adjacent Argentina (Peña, 1981), as well as in *Nothofagus* and *Arucaria* forests of Chile. Adults are seemingly active from November to March. We have seen only 19 specimens representing the following records:

ARGENTINA. *Neuquen*. Lago Tramen, 1000 m, III; XI; XII. San Martin de los Andes, XII. *Tucuman*. Tucuman (questionable location). *Locations Unknown*: "Patagonia", no data, 4. "Pampas", no data. "Salinas Chicas", no data (in Berg, 1901). LPMCN.

CHILE. *Curico*. Cordillera de Teno. *Malleco*. 6.5 km E Malalcahuello, 1080 m, *Nothofagus* forest, XII. 14 km E Malalcahuello, 1570 m, *Nothofagus* and *Aurucaria* forest, XII. Laguna Jesus-Maria and Pino Hachado (records of Peña, 1981). *Maule*. No data, 3. *Valdivia*. No data. No locality, 2. AFNC, BMNH, MNSC, SBPC.

Nicrophorus olidus Matthews

Figure 52; Map 15

Nicrophorus olidus Matthews, 1888: 92. Type locality: Mexico. Type in: BMNH, seen.

Diagnosis.— Length 10 – 14 mm. Pronotum orbicular with wide lateral and basal margins. Apical three antennomeres orange-red. Metasternal pubescence moderately dense, dark brown; metepimeron with a few short brown hairs. Hind tibia very slightly curved. Elytron with epipleural ridge short, not extending to apex of scutellum; dorsal surface with long dense hairs. Metatrochanter with sharp spine. Elytra with pattern as in figure 52.

Natural history and distribution.— The species is known only from Mexico north of the Isthmus of Tehuantepec. Adults have been collected from May to November. It occupies open forests, cloud forests, and rainforests. We do not accept Portevin's (1926) statement that the species occurs in Central America and Colombia. We have seen 267 specimens representing the following records:

MEXICO. *Durango*. 66 km SW La Ciudad de Durango, 2250 m, VI, 6. Revolucioneros, VII, 3 (location unknown). *Guerrero*. Omilteme. Xucamanatlan. *Hidalgo*. 10 km S Tenango de Doria, 3000 m, VII, 2. *Jalisco*. Ajijic, 1567 m, V, 3; XI, 2. 9.5 km W Atenquique, 1677 m, XI, 12. 13 km W Atenquique, 1799 m, IX, 15 km SW Autlan, 1312 m, IX, 30. 19 km SW Cocula, IX, 6. El Rincon, Los Volcanes, 1647 m. Cd. Guzman (L. de Zapotlan). *Mexico*. 5 km NE Temascaltepec, 1922 m, IX, 5. 9.6 km. NE Temascaltepec, 2135 m, IX, 2. Tenancingo, 2165 m, IX. *Morelia*. 12 km E Cuernavaca, VII. *Nuevo Leon*. Iturbide, 1800 m, VII, 2. 26 km W Linares, 671 m, V. *Oaxaca*. 11 km E Hautla. Juquila Mixes, XI, 4. 14.5 km NE Oaxaca, 1891 m, VIII, 7. 84 km S Oaxaca, V, 2. Sierra Madre del Sur, Escondido Road Crest, VI, 14. 24 km from Sola de Vega, 1830 m, V. Suchixtepec. 21 km S Valle Nacional, 1098 m, VII, 16; VIII, 8. 24 km S Valle Nacional, 1220 m, V. *Puebla*. 7 km SW Huachinango, 1700 m, VII, 2. Nuevo Necaxa, VII, 3. *Queretaro*. 29 km E Landa de Matamoros, 1617 m, VI, 3. 32 km W Xilitla, VI. *San Luis Potosi*. 17.5 km W El Naranjo, 960 m, VI, 25. 20 km W Xilitla, 1600 m, cloud forest, VI-VII, 3. 22.5 km W Xilitla, 1312 m, VI, 3. *Tamaulipas*. 10 km W El Encino, 2000 m, cloud forest, VII. Gomez Farias, 300 m, tropical deciduous forest, VI-VIII, 34; Rancho del Cielo, cloud forest, 1000 m, VI-VIII, 25; 1129 m, VII, 27. *Veracruz*. Cordoba. Tuxtla. 1.9 km S Huatusco, 1344 m, VIII, 2. 7 km N Huatusco, 1281 m, VIII, 3. 8 km W San Andres Tuxtla, VII.

Nicrophorus scrutator Blanchard

Figure 53; Map 14

Nicrophorus scrutator Blanchard, 1840: 74, in Brullé and Blanchard, 1840. Type locality: Bolivia. Type in: MNMN?, not seen.

Diagnosis.— Length 17 – 22 mm. Pronotum orbicular, with wide lateral and basal margins. Apical three antennomeres orange-red. Metasternal pubescence dense, dark brown; metepimeron with a few short brown hairs. Hind tibia very slightly curved. Elytron with epipleural ridge short, not extending to level of scutellar apex; dorsal surface with only a few long hairs, majority confined to lateral margins. Metatrochanter with spine reduced, broadly rounded. Elytron with pattern as in figure 53.

Variation.— A single specimen from Machu Pichu, Peru (in MZUSP) has an epipleuron with slightly more than the anterior half orange-red and the two fasciae on each elytron are confluent along the epipleural margin. This specimen also has typical brownish metasternal pubescence and the last three antennal segments are orange-red.

Natural history and distribution.— The species occurs in Peru, Bolivia and northwestern Argentina, seemingly in both open semi-arid and moist forested habitats. It is active from October to April. We have seen 40 specimens representing the following records:

ARGENTINA. *Catamarca*. Andalgalá, 4. Cuesta Mina Capillas (not located), 3200 m, II. Las Estancias (not located), I. San Angelo (not located), II. *Jujuy*. Jujuy, II. Volcan. *Misiones*. No data, questionable record. *Salta*. Anta, XII. 20 km N La Caldera, El Ucumar, 780 m, I; II. Cerillos, 1200 m, X. *Tucuman*. Ciudad Universitaria, San Javier, Tucuman, II. Horco Molle, 12 km W Tucuman, 700 m, I. Infiernillo, III. Mala-Mala, 2000 m, IV. Parque Aconquija, IV. Quebrada de Lules, III, 3; XII. Rio Pueblo Viejo, 1000 m, humid forest. San Pablo, 1200 m, 2. Siambon, II; VII. Tafi Viejo. Tucuman, VI; no date, 2. Villa Nouques, V; XII. Villa P. Mont, Burayacu. BMNH, FMLC, LPMC, SBPC.

BOLIVIA. *Chuquisaca*. La Laguna, Neubo Mundo Mountains, XII (Brullé and Blanchard, 1840). Tiguipa, IV. Pando. Rio Negro, II, doubtful record. *Santa Cruz*. Valle Grande (between Chilan and Tasajos, X (Brullé and Blanchard, 1840: 74). No data, 2. BMNH, MNHN.

PERU. Cuzco. Machu Pichu, 2600-2800 m, VII. MZUSP.

PHYLOGENY AND ZOOGEOGRAPHY

In this section we discuss the phylogenetic and geographic relationships of the Latin American silphid fauna and propose hypotheses about its origin.

RECONSTRUCTED PHYLOGENY OF *OXELYTRUM*

Ranges of all silphines of Latin America (listed in table 1), except *Oxelytrum*, extend into Mexico from the north and terminate at or before the southern edge of the Mexican Neo-Volcanic Plateau. Of these genera, only *Heterosilpha* is endemic to North America. All other genera have the majority of their species and ranges in Eurasia. A phylogenetic analysis of these genera can best be accomplished by including the Palearctic and Oriental species and will not be attempted here.

We do, however, present a reconstructed phylogeny for all members of the wholly New World genus *Oxelytrum* (fig. 56). *Oxelytrum* is identified as a monophyletic group on the basis of possession of the derived character state of presence of coxal spines or tubercles. Two lineages, each including four species, are recognized within *Oxelytrum*. One lineage, the *lineatocolle* group, is characterized by the derived character state of a black pronotum. It is associated with western coastal lowland and Andean montane habitats. Members of the other lineage, the *emarginatum* group, share the derived character state of a pronotum with reflexed margins, and a generally very similar overall habitus. It is associated with eastern and northern montane and lowland habitats.

The character analysis uses only adult characters (table 3) and is based on out-group comparison with the silphine genus *Ptomaphila* of Australia and New Guinea. These two genera are considered to compose a monophyletic group based on their shared possession of the derived character states of long hairs on the underside of the elytra near the apical callus, and a pronotum with elevated costae. These character states appear in no other Silphinae. We interpret these two genera as otherwise comparatively primitive, of great antiquity and derived from a common Gondwanaland ancestor.

Oxelytrum characters.— Characters used are those of taxonomic value. Whether all such characters are valuable as indicators of phylogenetic relationships is questionable. Characters have not been objectively weighted. As virtually all characters have unknown biological significance, it is not known how prone they are selective pressures promoting homoplasy. Nevertheless, gross inferences have been made concerning the degree of homoplasy expected in each character (Table 3).

Character 1, pronotum—dorsal surface. Two character states have been identified. Because elevated costae are not known in other Silphinae aside from *Oxelytrum* and *Ptomaphila* this state is interpreted as apotypic and of high weight.

Character 2, elytra—undersurface. Two character states have been identified. Because long hairs in the region of the apical callus are unknown in other Silphinae this state is interpreted as apotypic and of high weight.

Character 3, elytra—apex. Two character states have been identified. An internal flange is well-developed in members of *Ptomaphila* and lacking in *Oxelytrum* species. No other Silphinae possess such a feature, considered here as apotypic, although development of similar structures do occur in other Coleoptera probably as means of locking the elytra together at the

apex.

Character 4, head—frons. Three character states have been identified although there is variation in the degree to which the frons is swollen. In most other Silphinae, the frons is uniformly swollen while in *Oxelytrum* species a “v-shaped” swollen area (chevron) is present. *Ptomaphila* species lack any degree of swelling on the frons. Because the frons is swollen in members of Nicrophorinae, lack of or reduction in swelling is interpreted as apotypic. Tendency towards reduction in swelling could also be interpreted as further evidence of sister-group relationship between *Oxelytrum* and *Ptomaphila*.

Character 5, elytra—dorsal surface. Two character states have been identified although within species of *Oxelytrum* and other Silphinae, there is variation in the degree of elevation of costae. Presence of tubercles arranged linearly in place of costae (latter are only vaguely defined) is interpreted as apotypic. Linearly placed tubercles are lacking in all other Silphinae although tubercles interspersed between costae are known in species of *Thanatophilus*.

Character 6, elytral epipleuron—width. Two character states have been identified. Because a narrow epipleuron is found in most Silphidae this state is considered plesiotypic.

Character 7, coxae—ornamentation. Two character states have been identified: lack of any ornamentation and, presence of ornamentation as tubercles or spines. Because spines and tubercles are not known in other Silphinae, presence of these structures is considered apotypic.

Character 8, pronotum—color. Four character states have been identified. Because members of *Ptomaphila* possess a pronotum with the margins orange-red and disc black, presence of this state in *Oxelytrum* species is considered plesiotypic. An entirely black pronotum is interpreted as apotypic. Presence of a black pronotum with the posterolateral corners orange-red is interpreted as autapotypic and derived from an entirely black pronotum. A fourth character state is represented by a reduction in the size of the central black spot on the disc. Pronota with colored margins are known in species of other silphine genera but it is not known if they represent sympleisiomorphy or secondary apotypic developments. Although the sole basis for recognizing monophyly of the *lineatocolle* group, it should be emphasized that this is a character likely prone to convergence and should thus be considered accordingly.

Character 9, eyes—size. Two states have been identified. Because large eyes are found in species of *Ptomaphila*, this state is considered plesiotypic. Eye size is undoubtedly correlated with diel activity patterns. Nocturnal species have large eyes; diurnal species small eyes. Accordingly this character is extremely prone to homoplasy and should be weighted accordingly.

Character 10, pronotum—posterior angles. Two states have been identified. Because obtuse angles are known in species of *Ptomaphila* and most other Silphinae, this state is considered plesiotypic.

Character 11, female genitalia—stylus. Two states have been identified. Because aberrant scoop-like styli are unknown in any other Silphinae, they are considered apotypic. Whether the modification of the styli represents a change in oviposition habits is not known.

Character 12, coxae—ornamentation. Two states have been identified. Spines and tubercles on the coxae are not known in other Silphinae. Presence of spines is considered apotypic because they represent a likely progression from an ancestor which possessed tubercles, the plesiotypic state. Consideration of spines as apotypic is also compatible with distribution of states of character 11 and with overall similarity of members of the group being defined.

Character 13, pronotum—margins. Three states have been identified. Because flat or deflexed pronotal margins are known in other Silphinae, including *Ptomaphila*, reflexed

margins are considered apotypic. States of this character represent apparently simple changes and are probably prone to homoplasy. Distribution of states of this character is the sole basis for recognizing the monophyly of the *emarginatum* group, and the latter should be considered accordingly.

Character 14, abdominal segments of male—lateral margins. Two states have been identified although there is variation in species of *Oxelytrum* in the prominence of the lateral projections. Because lateral projections are unknown in other Silphinae, their occurrence in species of *Oxelytrum* is considered apotypic. The reduced prominence of the projections in *O. discicollis* are interpreted as secondarily reduced and autapotypic.

Character 15, elytra—humeri. Two states have been identified. Toothed humeri are known in some species of *Oiceoptoma*. However, they are not known in *Ptomaphila* or other Silphinae and thus likely represent independent developments. Presence of a tooth on the humerus in species of *Oxelytrum* is therefore considered apotypic but possibly homoplasious.

Character 16, pronotum—color. Four states have been identified. Two of these have been considered previously. A pronotum with the central black spot markedly reduced in size is considered apotypic, derived from a similarly colored pronotum with the black spot larger in size.

RECONSTRUCTED PHYLOGENY OF *NICROPHORUS*

We present here a phylogenetic analysis of the relationships of all species of *Nicrophorus* in the New World (listed in table 2), based upon both adult and, where available, larval characters (tables 4-7 and figures 57-60). Larval characters and interpretations of their polarity are from Anderson (1982a). The adult characters, habitats, and distributions of the Nearctic species are from Anderson and Peck (1985), and are interpreted for the first time here. Polarization of all larval and adult character states in *Nicrophorus* are based on out-group comparison with the Asian genus *Ptomascopus*, the only other genus in the subfamily Nicrophorinae. We also make predictions about phylogenetic affinities of some *Nicrophorus* species which are testable by the discovery and description of their larvae.

Since only New World species of *Nicrophorus* are considered, the cladograms may require subsequent modification when Old World species are included. This will be especially so if the New World component of a particular species group is found not to be monophyletic. Hatch (1927) gives a start at an evolutionary analysis, but his assignment of *Nicrophorus* species into groups was based on shared ancestral characters (symplesiomorphies) and on characters which we believe are subject to convergence. We agree with his placement of some species, but dispute others. Since we have not carefully studied many Palearctic species, we refrain from including any of these in our delimited species groups although we think that at least some Palearctic species are easily placed in our groups. We do not attempt to demonstrate relationships between species groups. This can only be reliably accomplished following examination of all *Nicrophorus* species.

The *orbicollis* group

This species group is characterized by the uniquely derived adult character states of a short elytral epipleural ridge and by most members having prominent hairs on the dorsal surface of the elytra. We place six New World species in this group and propose phylogenetic relationships as in table 4 and figure 57. Larvae of all Latin American species are undescribed.

orbicollis group characters.— Character 1, elytral epipleuron—length. Two character states have been identified. Because a long elytral epipleuron occurs in *Ptomascopus* species and Silphinae, this state is considered plesiotypic. A short epipleuron is also known in some southeast Asian species of *Nicrophorus*, however the relationships of these species to members of the *orbicollis* group have yet to be assessed.

Character 2, pronotum—shape. Four character states have been identified in *Nicrophorus* species. For *Nicrophorus*, a cordate pronotum is considered plesiotypic because this is the state which occurs in species of *Ptomascopus*. Among subquadrate, quadrate and orbicular pronota, we hypothesize the subquadrate condition as plesiotypic, directly derived from a cordate pronotum. We believe that quadrate and orbicular pronota each represent unique apomorphic states derived directly from the subquadrate state. Alternative interpretations are perhaps equally likely concerning the position in the transformation series of the orbicular pronotum. Alternatively, this state could be directly derived from the primitive cordate state. We find the former alternative to be most compatible with distribution of states of other characters.

Characters 3,5,6 elytron—vestiture of dorsal surface. Five character states concerning the nature of the dorsal vestiture have been identified in *Nicrophorus* species. A dorsal surface with very few or no hairs is considered plesiotypic because this state also occurs in species of *Ptomascopus*. We hypothesize increasing density of the hairs as increasing degrees of apotypy. Hairy elytra are also known in some southeast Asian species of *Nicrophorus*. However, the relationships of these species to members of the *orbicollis* group have yet to be assessed.

Character 4, metatrochanter—ornamentation. Two states have been identified in *Nicrophorus* species. Because a metatrochanter with a sharp, well-developed spine is known in other *Nicrophorus* and *Ptomascopus* a reduced, blunt spine is considered apotypic.

Character 7, elytral epipleuron—vestiture. Three character states have been identified in *Nicrophorus* species. Because an epipleuron with a few short hairs is known in *Ptomascopus* species, this state is considered plesiotypic. Occurrence of a densely hairy epipleuron is probably correlated with a densely hairy elytral dorsal surface, and is considered apotypic.

New World members of this group are associated with forested or open habitats in both North and Latin America. This species group appears to have its center of diversity in Latin America, with only one New World species being distributed north of Mexico. All species of *Nicrophorus* known from southern Central and South America belong to this group. This may indicate that the group is endemic to the New World and that the species evolved from an early lineage within *Nicrophorus*. This latter suggestion is supported by the plesiomorphic condition of larval character states of *N. orbicollis* (Anderson, 1982a).

According to Portevin (1920a, 1926), the derived character states of short epipleural ridges and hairy elytra are also known to occur (at least in part) in *N. distinctus* Grouvelle (Sulawesi (= Celebes) Islands), *P. heurni* Portevin (New Guinea), and *N. podagricus* Portevin (Borneo and Sulawesi) and also in *N. kieticus* Mroczkowski (1959) from the Solomon Islands. The relationship of these southern Indo-Malayan species to our *orbicollis* species group may be of importance for subsequent biogeographic interpretations to be discussed later.

The *defodiens* group

This species group can be defined by the uniquely derived larval character states of narrowly separated labial palpi with the basal segment ventrally unsclerotized.

defodiens group characters.— Character 1, larval labial palpi—relative position of bases. Two states have been identified. Because labial palpi with widely separated bases are known in

Ptomascopus morio, this state is considered plesiotypic.

Character 2, larval labial palpi-sclerotization of basal segment. Two states have been identified. Because labial palpi with a sclerotized ventral surface of the basal segment are known in *Ptomascopus morio*, this state is considered plesiotypic.

Character 3, pronotum-shape. See discussion of Character 2 in the *orbicollis* group.

Character 4, adult antennomeres 9,10-setosity. Two character states have been identified. Because white setae on the ventral surfaces of antennomeres 9 and 10 are not known in *Ptomascopus* species or other *Nicrophorus* species, this state is considered apotypic. Dense setae, arranged in a "figure eight" pattern are autapotypic in *N. vespilloides*.

We place three New World species in this group and their relationships are indicated in table 5 and figure 58. New World members are associated with northern Nearctic forested and swampy habitats. No species in the group is known or suspected to occur in Latin America.

The *investigator* group

This species group can presently best be defined by the uniquely derived character state of a prepupal overwintering stage. In *N. mexicanus* and *N. nigrita* there are no known overwintering stages but the species are most active in fall, winter and spring seasons suggesting descent from an ancestor with a prepupal overwintering stage. Both *N. nigrita* and *N. investigator* share the derived larval character of a sclerotized ventral apex of abdominal segment 10.

investigator group characters.— Character 1, overwintering stage. Two stages have been identified based on studies of populations at northerly latitudes. We hypothesize overwintering as an adult as plesiotypic and expect that it occurs in *Ptomascopus*. Southerly species that are fall-through-spring active are considered derived from a northern ancestor which had a prepupal overwintering stage.

Character 2, adult metasternum-vestiture. Two states have been identified. Because a uniformly pubescent metasternum is known in *Ptomascopus* species and all other *Nicrophorus* species, this state is considered plesiotypic.

Character 3, larval abdominal segment 10-ventral apex. Two states have been identified. Because an unsclerotized apex is known in *Ptomascopus* species and all other *Nicrophorus* species, this state is considered plesiotypic.

Character 4, pronotum-shape. See discussion of Character 2 in the *orbicollis* group.

Character 5, adult metasternum-color of vestiture. Two states have been identified. Because yellow pubescence is found in primitive *Nicrophorus* species, this state is deemed plesiotypic within the *investigator* group. Yellow pubescence may be apotypic for the genus *Nicrophorus* because *Ptomascopus* species possess brown pubescence. Distribution of states of this character in all *Nicrophorus* species suggests a high degree of homoplasy and cautions against its overemphasis. Distributional data on *N. mexicanus* and *N. nigrita*, and uniformity of habitus, also support a sister-species relationship between these two species.

We place five New World species in this group and their relationships are indicated in table 6 and figure 59. Larvae of *N. mexicanus* are undescribed but are expected to possess the derived character states in table 6 based upon our interpretation of its phylogenetic position with respect to other members of this group. New World members of the group are associated with open, sparsely forested, and densely forested habitats throughout North America. Within this group only *N. mexicanus* and *N. nigrita* have ranges extending into Mexico. *N. nigrita* occurs not only on the mainland of Baja California, but has dispersed 250 km to Guadalupe

Island. It has also crossed smaller water gaps to the California Channel Islands. *N. mexicanus* extends throughout the Mexican Plateau and into Guatemala. It and *N. marginatus* are the only species of *Nicrophorus* with an extensive distribution in both the United States and Latin America.

The *marginatus* group

This species group is defined by the uniquely derived adult character state of dense yellow hairs on the posterior lobe of the metepimeron and the derived larval character state of an unsclerotized base of the venter of abdominal segment 10.

marginatus group characters.— Character 1, larval abdominal segment 10—ventral base. Two character states have been identified. Because a sclerotized base occurs in *Ptomascopus* species, this state is considered plesiotypic.

Character 2, adult metepisternum, posterior lobe—pubescence. Three states have been identified in *Nicrophorus* species. Because a metepimeral lobe with a few sparse hairs is known in *Ptomascopus* species, this state is considered plesiotypic.

Character 3, larval abdominal segment 9—sternite. Two states have been identified. Because a sternite with the outer angles acute is known in *Ptomascopus morio*, this state is considered plesiotypic.

We place three New World species in this group and their relationships are shown in table 7 and figure 60. A fourth, *N. carolinus*, is tentatively placed within this group although adults lack the above derived characters and larvae are undescribed. However, we suspect that *N. carolinus* is phylogenetically close to the *marginatus* group based on its overall habitus and retention of some ancestral character states, shared with members of the *marginatus* group. We predict that larvae, when described, will support these suspicions (fig. 60). New World members of the group (excluding *N. carolinus*) are primarily associated with open habitats throughout western North America. Within the group, only *N. marginatus* has a distribution which extends into the arid regions of the northern half of the Mexican Plateau.

Incertae Sedis

At present we are unable to assign the North American *N. americanus* and *N. pustulatus* to definable New World species groups. This is partly due to the fact that larvae are undescribed for both species, and that adults retain primitive states for all characters used to define the above groups. Our inability to assign these species to groups may also be because they have no other relatives in the New World, as has already been suggested for *N. americanus* by Anderson (1982c).

ZOOGEOGRAPHY AND SPECIES ORIGINS

Silphinae other than Oxelytrum.— Genera and their number of included species in North America north of Mexico are as follows: *Necrodes* (1), *Thanatophilus* (5), *Aclypea* (2), *Oiceoptoma* (3), *Heterosilpha* (2), and *Necrophila* (1). Of these, only *Heterosilpha* is endemic. We assume all but *Heterosilpha* to have originated in the Palearctic region because this is where their highest species diversity is, and where several additional related genera occur. We assume that members of these genera independently invaded North America at least five different times in the Tertiary, probably across the Bering Land Bridge, but alternatively across North Atlantic land bridges, before the opening of this ocean in the early Tertiary

(Matthews, 1979). There is no evidence that any of these silphine genera occurred in Latin America any farther south than the edge of the Mexican Plateau. In these genera, the sole endemic Latin American species, *T. graniger*, is readily interpreted as a southern isolate of *T. lapponicus* or its ancestor, which reached the uplands of the Mexican Plateau and the Transverse (or Neo) Volcanic Sierra in a cooler glacial climate, and became isolated there in a warmer interglacial.

Latin American silphid fossils are not known. Hatch (1927) reviewed the known Mesozoic and Tertiary fossils known to that time and attributed to Silphidae. They tell little about the origin of extant North American or Latin American genera. This is also true of the recent review of Russian Mesozoic beetles (Arnoldi *et al.*, 1977).

Oxelytrum.— The sister group relationship of a Latin American genus (*Oxelytrum*) and an Australian genus (*Ptomaphila*) is a pattern known in many insect and other groups (reviewed in Keast, 1973). This pattern can be best interpreted as resulting from separation of an ancestral distribution on at least part of the southern Mesozoic supercontinent of Gondwanaland following its breakup during the Cretaceous. Temperate lands remained in proximity between Australasia and South America into the Eocene (50 million years BP), some 40 million years after their separation from Africa, and 30 million years after the separation of New Zealand (Raven and Axelrod, 1975). No other closely related silphine genera occur on the other present or formerly southern main land masses of New Zealand, Africa, Madagascar, or India. We suggest that *Oxelytrum* diversified and speciated after the separation and isolation of South America from other southern land masses.

We suggest initial divergence of this *Oxelytrum* stock into two lineages; the *lineatocolle* group in more western coastal lowland habitats, and, the *emarginatum* group in more northern and eastern lowland habitats.

The *lineatocolle* group probably had an ancestral species possessing many character states similar to those of *O. lineatocolle* and may have originally occupied temperate habitats such as *Nothofagus* forests along the western coast of South America. We hypothesize that the first phase of the Andean orogeny during the late Cretaceous may have provided the earliest set of barriers allowing for the divergence of this lineage into two descendant forms. One of these is currently represented by *O. lineatocolle* in the south-central Chilean coastal lowlands and Andean slopes. The other, perhaps a more inland and higher elevation form, representing the ancestor of the remaining three species in this group, underwent subsequent divergence into (1), a more southerly cold-temperate, but lower-elevation montane form, and (2), a more northerly cold-adapted high-elevation montane form. This perhaps occurred during the second phase of Andean orogenic activity and formation of high elevation grassland habitats. The first is presently represented by *O. biguttatum* in extreme southern Chile and Argentina. The second represents the ancestor of *O. apicale* and *O. anticola* which probably inhabited the high elevation grasslands and steppes of Argentina, Bolivia, Ecuador and Peru. A possible early Pliocene or Pleistocene isolation of northern and southern forms, perhaps as a result of glacial events (Noonan, 1981), is indicated by the descendant species, the more northerly *O. anticola* and the more southerly *O. apicale*, allopatrically distributed in these high Andean open habitats.

In the *emarginatum* group, the ancestral species probably possessed many character states similar to those of *O. emarginatum* and may have occupied the lowland forests of northern, central and eastern South America. We hypothesize isolation of a more upland form in the southern Brazilian Highlands, presently represented by *O. emarginatum*, and a widespread

northern lowland form representing the ancestor of the remaining three species in this group. This latter form diverged into southerly lowland northern lowland to middle elevation montane forms perhaps during the second phase of Andean orogeny in the mid-Tertiary. The southern lowland form is presently represented by the allopatric *O. erythrurum* and the other form represents the ancestor of the widespread, but largely allopatric, *O. discicolle* and *O. cayennense*. Divergence into these latter two species may also be due to continued Andean orogeny in the Pliocene or Pleistocene. *O. cayennense* is apparently limited to the lower montane and lowland Amazon Basin forests, while *O. discicolle* is distributed in forests of the surrounding regions at higher elevations. *O. discicolle* is the only species of *Oxelytrum* ranging into Central America and Mexico. This is probably the result of Pleistocene dispersal from montane areas of northern South America along the island-like montane habitats of Central America to Mexico. Although many recent interpretations of the evolutionary histories of Latin American taxa have emphasized the role of Pleistocene forest refugia caused by climatic changes in South and Central America (reviewed by Simpson and Haffer, 1978; Prance, 1982; Whitehead, 1976; but for an alternative view see Endler 1982) in promoting speciation we believe that species origins of all Latin American Silphidae, with the possible exception of *Thanatophilus graniger*, predate the Pleistocene.

Nicrophorinae.—The full biogeographic history of *Nicrophorus* can be presented only after the Eurasian fauna has been extensively studied. The sister genus of *Nicrophorus* is *Ptomascopus* of eastern Asia whose adults exhibit more primitive states of structural characters and have not evolved advanced parental care of the larvae, as is found in members of *Nicrophorus* (Peck, 1982). The genus *Nicrophorus* seems to be Eurasian in origin because this is where the sister genus occurs, and because more species of *Nicrophorus* occur in Eurasia (about 60) than in the New World (20). No species are known to occur in Australia or sub-Saharan Africa.

We suggest that each of the four species groups, plus *N. americanus* and *N. pustulatus*, may represent one or more ancestral invasions of North America via the Bering or North Atlantic Land Bridges during the Tertiary or Pleistocene. Only two species, *N. vespilloides* and *N. investigator*, are in both North America and Eurasia, occupying far northern localities. Both probably occurred on and moved freely across the Bering Land Bridge during low sea stands in the Pleistocene.

Somewhat more than half of the North American species live in deciduous forests of the eastern and southeastern United States. We interpret this to be suggestive of the ancestral habit. Occupation of North America by species ancestral to these can therefore date to the early Tertiary when such forests were continuous from Asia, across Beringia, to North America or alternatively from Europe, directly to eastern North America (see Matthews, 1979, 1980 for review).

Grassland and open shrub habitats seemingly started to become abundant in North America in the Miocene, as a result of the formation of large rain shadows caused by the uplift of the Rocky Mountains. We suggest that species occupying these more open and semi-arid environments are younger and more derived, or represent later ancestral invasions. Except for the *orbicollis* group, only these species of more open and arid habitats have entered northern Mexico, and most of them range no farther south than the edge of the Mexican Plateau. We suggest only a Pleistocene or Recent occupation of Mexico by these species. The single exception, *N. mexicanus*, reaches Guatemala and El Salvador.

Only the *orbicollis* group of *Nicrophorus* contains species endemic to Latin America. This group may be the earliest to enter North America from Eurasia due to its apparent primitive position with respect to other species groups, and its association primarily with hardwood forested habitats.

The basal stock of the *orbicollis* group would seem to possess character states similar to those of *N. chilensis* (fig. 57). This stock probably reached South America from North and Central American ancestors in the date Cretaceous or early Tertiary while the two areas were still connected, or by over-water dispersal as is proposed for some island-hopping mammals in the early or mid-Tertiary (Darlington, 1957; Simpson, 1980). Alternatively, arrival of the *orbicollis* group of *Nicrophorus* in South America may date from the early Pliocene, and be contemporaneous with the start of the "Great American Interchange" of faunas. At this time the Andes were considerably uplifted, but not to their present height. By late Pliocene the Panama seaway was closed and additional uplift of the Andes formed a continuous temperate Andean dispersal corridor (Haffer, 1974; Simpson, 1980).

Diversification and endemism of Central and South American *Nicrophorus* species argues for an early rather than late entry into Central and South America. There is no evidence to suggest that *Nicrophorus* reached South America from the south, when it was part of the Gondwanaland supercontinent, although Melville (1981) discusses plant taxa with South American and Indo-Malayan affinities and interprets them as parts of a fragmented hypothesized supercontinent called Pacifica. We have not closely examined Old World relationships of the *orbicollis* group. They may lie with some southeast Asian species and may be another example of this type of distribution pattern. Alternatively, such relationships may be taken as evidence of a more widespread distribution of the members of this species group than initially thought.

After reaching South America, the *Nicrophorus* ancestor seemingly remained in forested habitats and spread down the rising Andes chain to Chile. Here, perhaps due to the later development of an arid barrier across the Andes, an isolated population now represented as *N. chilensis* was formed. The remaining northern South American ancestral stock was again split with the development of two isolated forest regions separated partly by the high Andes. We suggest that this produced *N. scrutator* on the eastern flanks, in Peru, Argentina and Bolivia, and *N. didymus* with a range generally in more northerly Andean forests.

We finally suggest that the ancestor of the remaining three species in this group was distributed throughout warm-temperate or subtropical humid forests from eastern North America, through Mexico to at least Guatemala, if not Panama. Many organisms, and especially species or species pairs in tree genera such as *Fagus* (Beech), *Liquidambar* (Sweetgum), *Cercis* (Redbud), *Carpinus* (Blue Beech), and *Ostrya* (Ironwood), show this former Tertiary distributional connection across the present broad and arid barrier formed by the Rio Grande depression (see Martin and Harrell, 1957; Rosen, 1978; Allen and Ball, 1980). The formation of this arid barrier in the late Tertiary allowed for the concurrent isolations of *N. orbicollis* in the United States, and populations in Mexico through to Panama which subsequently gave rise to the allopatric *N. olidus* in humid upland forests in Mexico north of the arid lowland barrier of the Isthmus of Tehuantepec, and *N. quadrimaculatus* in the upland forests between the Chiapas highlands and western Panama.

BIOGEOGRAPHIC SYNTHESIS

Latin American silphid species can be grouped into four categories based upon distribution (modified from Savage, 1982): 1), Widespread—A single species found throughout Middle and South America; 2), South American—Ten species endemic to South America; 3), Middle America—One species endemic to Central America, two endemic to Mexico; and 4), Extratropical North American—Ten species found largely in North America but whose ranges extend at least in part into Mexico or northern Central America.

Many entomologists do not realize that silphids are present in Latin America. This is perhaps because the necrophagous niche has been extensively exploited by Scarabaeidae possibly due to a comparative lack of large herbivores which supply the fecal material for these beetles in other areas of the world. That the silphid presence in Latin America is of great antiquity is indicated by the endemic South American assemblage of species. Of the ten South American endemics, seven belong to the genus *Oxelytrum*, and three to the *orbicollis* group of *Nicrophorus*. The presence of these two groups in South America, however, is the result of two different historical pathways.

Oxelytrum, like many South American taxa, appears to owe its presence in South America to fragmentation of the supercontinent of Gondwanaland during the Cretaceous period. Species diversification of *Oxelytrum* occurred during the Tertiary while South America was in isolation. On the other hand, endemic species of *Nicrophorus* in South America appear to be the result of southerly movement from North America into South America perhaps during the late Cretaceous or early Tertiary while the two land areas were still connected. Alternatively, dispersal to South America could have taken place during the Tertiary over the island chain that is now Central America, as proposed for angiosperms by Raven and Axelrod (1974). The former appears preferable since the two Middle American endemic *Nicrophorus* are highly derived and have a North American sister-group and thus probably originated at some later time in the Tertiary through a second inter-island dispersal from a northern and not southern source.

Only a single species of *Oxelytrum* has dispersed from South America north into Middle America, but because no divergence has taken place between populations, it is likely that this was a Pleistocene event. No South American *Nicrophorus* have reached Middle America. The other Mexican endemic, *Thanatophilus graniger*, is readily interpreted as resulting from a Pleistocene isolation of northern ancestral form.

The ten remaining species are all extratropical North American with the greater part of their range in temperate North America, and in most instances they just range into the arid desert lands of northern Mexico. Only two species occur extensively in these arid areas, reaching as far south as the Neo-Volcanic Sierra. A third species, *Nicrophorus mexicanus*, ranges to El Salvador. Most of these species seem to be of recent origin, and probably evolved *in situ* in response to increasing aridity and cooling trends in the late Tertiary.

Thus the Latin American silphid fauna originated from a variety of sources during various time periods since the late Cretaceous. As with many Latin American taxa, South America possesses a characteristically more primitive and largely endemic assemblage of species. Central America is largely transitional with species found there either being widespread tropical or montane endemics of probable Tertiary origin and either direct North or South American ancestry. Mexico not only possesses endemics of this latter kind, but also species of more recent Pleistocene origin. A final significant portion of the fauna of Mexico is due to the

widespread nature of the distributions of species found in the arid southwestern United States.

SUGGESTIONS FOR FUTURE WORK

The present review has attempted to clarify understanding of the classification, phylogeny and zoogeography of Latin American Silphidae. We hope we have, at least in part, succeeded. During our work however, we soon came to realize that many aspects of Latin American silphids have not been well studied and warrant further attention. We think it important to outline some of the more interesting and potentially useful of these topics here in the hope that someone will find them stimulating enough to undertake.

First, we think life history studies of species of Latin American *Nicrophorus* and *Oxelytrum* should be undertaken. Not only will this provide missing basic biological information, but also other life stages including larvae, which can be subsequently used to test reconstructed phylogenies presented here by adding more characters for analysis. Second, comparative ecological studies should be undertaken to find out how silphids are interacting with other necrophagous arthropods in tropical, subtropical and south-temperate habitats and if their roles in carrion communities are similar regardless of locality. Third, patterns of color variation in some species of *Oxelytrum* and *Nicrophorus* should be examined, and the results considered within the framework of the Pleistocene forest refugium theory. These species represent needed further examples that could be used to support or discredit this now highly controversial theory. Finally, attempts should be made to provide more specimens, particularly of South American species. This will lead to increased resolution of species distributions and species chorological relationships. The latter especially, may play an important role in determining species geographic limits.

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Table 1. Classification of known or possible Latin American Silphinae.

Oxelytrum Gistel*lineatocolle* group*O. lineatocolle* (Laporte)*O. biguttatum* (Philippi)*O. apicale* (Brullé)*O. anticola* Guérin-Ménéville*emarginatum* group*O. emarginatum* (Portevin)*O. erythrurum* (Blanchard)*O. cayennensis* (Stürm)*O. discicolle* (Brullé)*Necrodes* Leach*N. surinamensis* (Fabricius)*Thanatophilus* Leach*T. graniger* (Chevrolat)*T. lapponica* (Herbst)*T. truncata* (Say)*Heterosilpha* Portevin*H. aenescens* (Casey)*H. ramosa* (Say)*Oiceoptoma* Leach*O. rugulosum* Portevin

Table 2. Classification of New World *Nicrophorus* species.*Nicrophorus* Fabricius*orbicollis* group*N. chilensis* Philippi*N. scrutator* Blanchard*N. didymus* Brullé*N. orbicollis* Say*N. olidus* Matthews*N. quadrimaculatus* Matthews*defodiens* group*N. sayi* Laporte*N. defodiens* Mannerheim*N. vespilloides* Herbst*investigator* group*N. tomentosus* Weber*N. hybridus* Hatch and Angell*N. investigator* Zetterstedt*N. nigrita* Mannerheim*N. mexicanus* Matthews*marginatus* group*N. marginatus* Fabricius*N. obscurus* Kirby*N. guttula* Motschulsky*N. carolinus* (Linnaeus)*Incertae sedis**N. americanus* Olivier*N. pustulatus* Herschel

Table 3. Analysis of character transformations in *Oxelytrum* - *Ptomaphila* lineage of Silphinae. Relationships only of species of *Oxelytrum* are shown in fig. 56. Species of *Ptomaphila* are not considered. Superscripts on characters indicate that we consider them to be homoplasious (1) or simple and unique (2). *Terms of Arnett 1944.

	character	plesiotypic character state	apotypic character state
1.	pronotum ²	without elevated costae	with costae
2.	elytral undersurface ²	lacking long hairs	with long hairs near apical callus
3.	elytral apex ²	lacking flange	with flange
4.	head ²	with v-shaped swollen area (chevron) on frons	lacking frontal chevron
5.	elytron ²	tricostate	tuberculate
6.	elytral epipleuron ²	narrow	extremely wide
7.	male coxae ²	without tubercles or spines	with tubercles or spines
8.	pronotum ¹	margin orange red, disc black	all black
9.	eyes ¹	large size	small size
10.	pronotum ¹	posterior angles obtuse	posterior angles rounded
11.	female genital coxites ^{2*}	with styli small, unmodified	with styli large, scooplike
12.	male coxae ²	with tubercles	with spines
13.	pronotum ¹	margins flat or deflexed	margin reflexed
14.	abdominal segments 4, 5 ¹ (of some males)	without lateral projections	with lateral projections
15.	elytra ¹	humeri not toothed	humeri each with single tooth
16.	pronotum ¹	black spot on disc large	black spot on disc reduced

Table 4. Analysis of character transformations in *orbicollis* group of species in *Nicrophorus*. Relationships of species are shown in fig. 57.

	character	plesiotypic character state	apotypic character state
1.	elytral epipleuron	long	short
2.	pronotum	subquadrate	orbicular
3.	elytron	dorsal surface glabrous, or with few short hairs	with long hairs
4.	metatrochanter	with spine sharp, well developed	with spine reduced, rounded
5.	elytron	hairs sparse	hairs dense
6.	elytron	hairs dense	hairs extremely dense, short
7.	elytral epipleuron	glabrous or with few short hairs	densely hairy

Table 5. Analysis of character transformations in the *defodiens* group of species in *Nicrophorus*. Relationships of species are shown in fig. 58.

	character	plesiotypic character state	apotypic character state
1.	larval labial palpi	bases widely separated	bases narrowly separated
2.	larval labial palpi	ventral surface of basal segment sclerotized	ventral surface of basal segment unsclerotized
3.	adult pronotum	subquadrate	quadrate
4.	adult antennomeres 9, 10	lacking white setae on ventral surfaces	possessing white setae on ventral surfaces

Table 6. Analysis of character transformations in the *investigator* group of species in *Nicrophorus*. Relationships of species are shown in fig. 59.

	character	plesiotypic character state	apotypic character state
1.	overwintering adult stage		prepupa
2.	adult metasternum	lacking bald spot	with bald spot immediately posterior to mesocoxae
3.	ventral apex larval abdominal segment 10	unsclerotized	sclerotized
4.	adult pronotum	sub-quadrate to cordate	quadrate
5.	adult metasternal pubescence	yellow	brown

Table 7. Analysis of character transformations in the *marginatus* group of species in *Nicrophorus*. Relationships of species are shown in fig. 60.

	character	plesiotypic character state	apotypic character state
1.	ventral base of sclerotized larval abdominal segment 10		unsclerotized
2.	pubescence of adult metepimeral posterior lobe	glabrous or with few hairs	dense yellow hairs
3.	sternite of larval abdominal segment 9	outer angles acute	outer angles truncate
4.	hairs on anterior face of adult procoxae	short	long

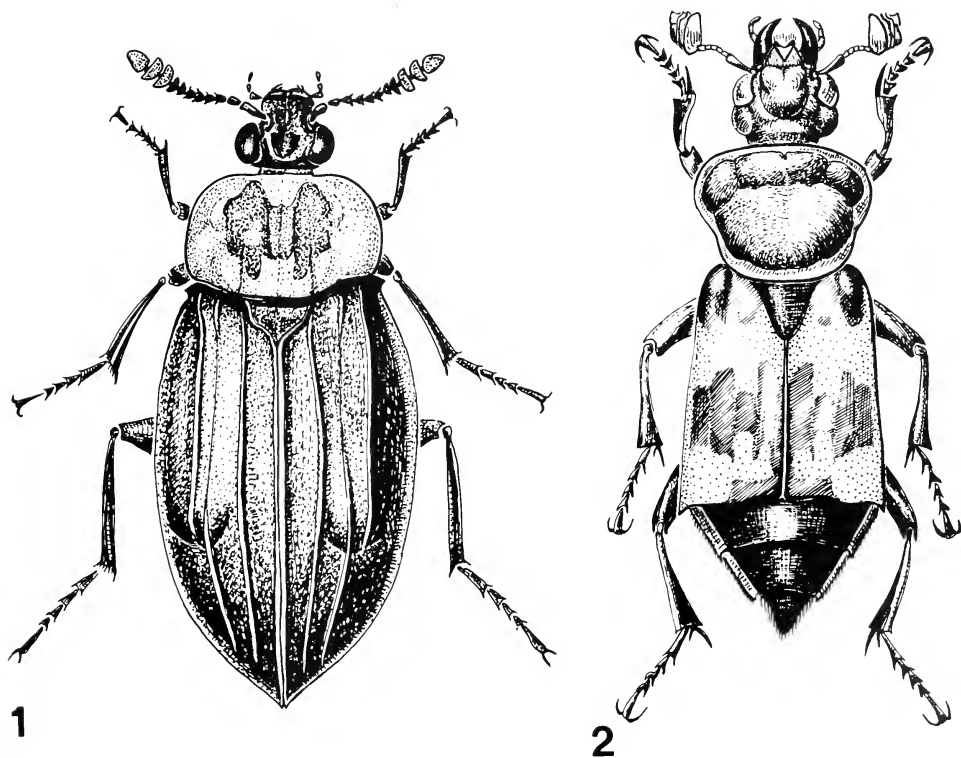
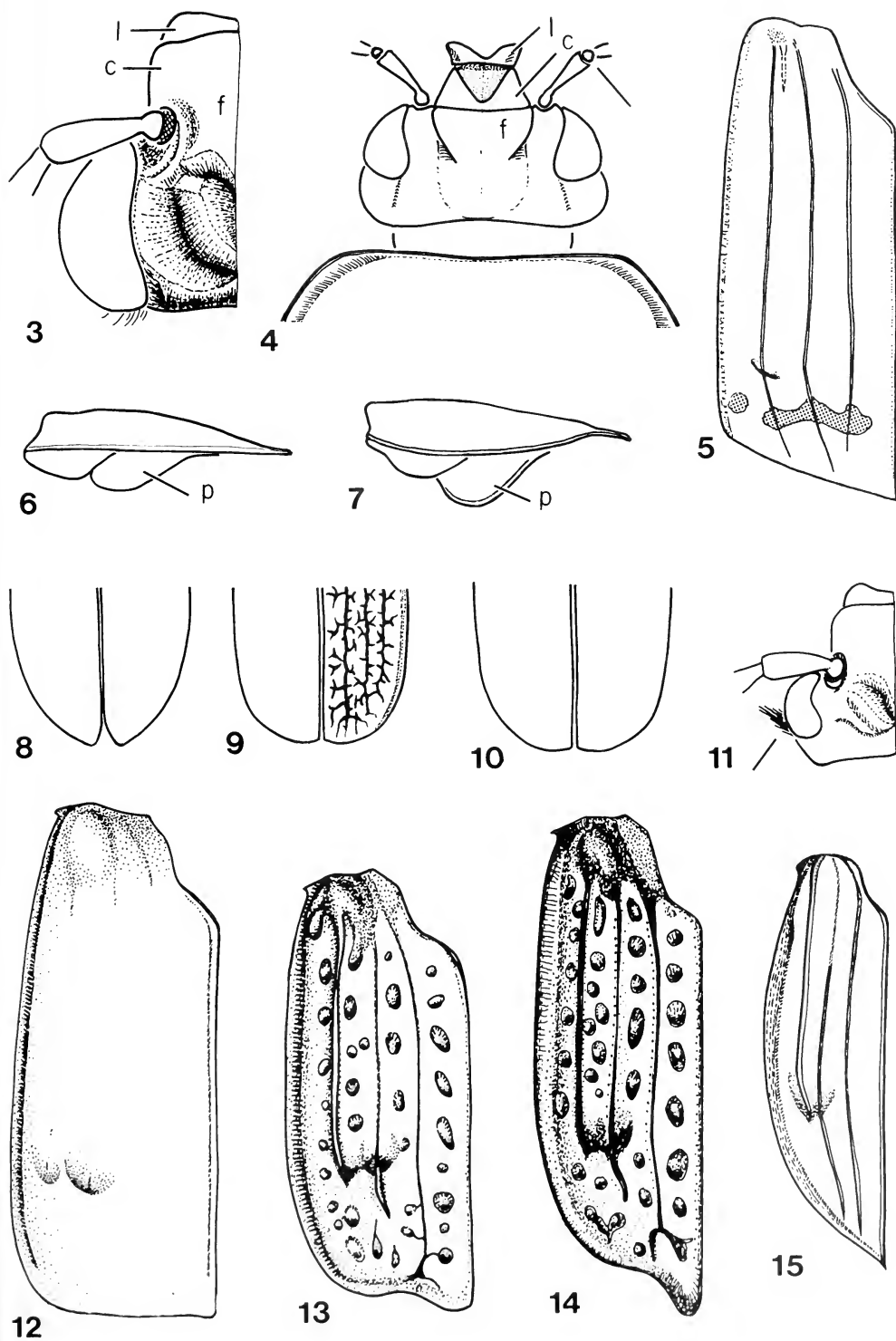


Plate 1. Figures 1, 2. Fig. 1. Habitus of *Oxelytrum discicollis*, body length 15 mm. Fig. 2. Habitus of *Nicrophorus marginatus*, body length 19 mm.

Plate 2. Figures 3-15. Fig. 3. Head of *Oxelytrum discicollae*: 1, labrum; c, clypeus; f, frons. Mandibles not drawn. Fig. 4. Head of *Nicrophorus marginatus*; symbols as in fig. 3; Note nicrophorine character of very small second antennal segment. Fig. 5. Right elytra of *Necrodes surinamensis* with apical reddish markings. Fig. 6. Short and broadly rounded pronotal postcoxal lobe (p) of *Necrodes surinamensis*. Fig. 7. Longer pronotal postcoxal lobe (p) of *Thanatophilus graniger*. Fig. 8. Pointed elytral apices of female *Heterosilpha ramosa*. Fig. 9. Reticulate sculpturing and rounded elytral apices of male *Heterosilpha ramosa*. Fig. 10. Rounded elytral apices of male and female *Heterosilpha aenescens*. Fig. 11. Head of *Oiceoptoma rugulosum*. Fig. 12. Elytron of *Thanatophilus truncatus*. Fig. 13. Elytron of female *Thanatophilus lapponicus*. Fig. 14. Elytron of female *Thantophilus graniger*. Fig. 15. Elytron of female *Oxelytrum discicollae*.



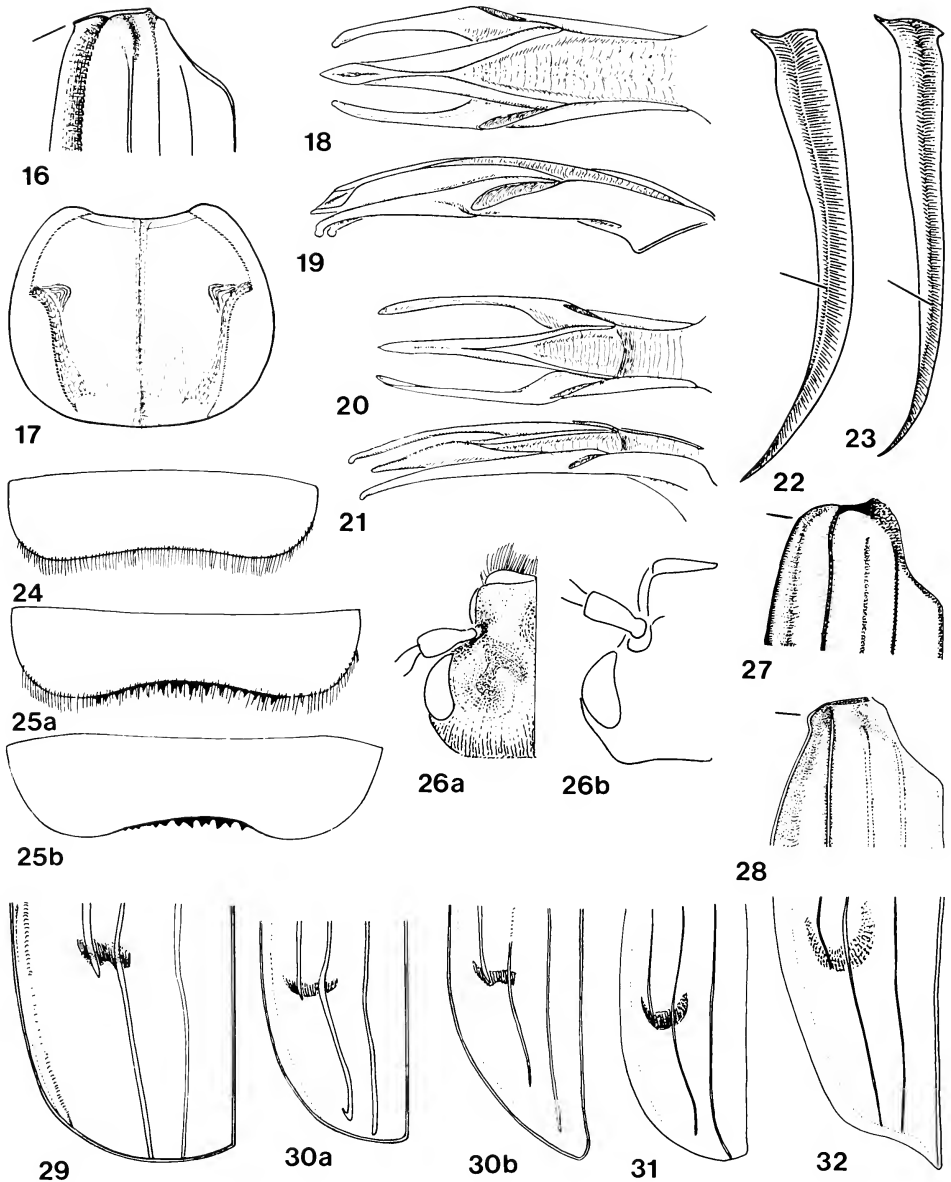


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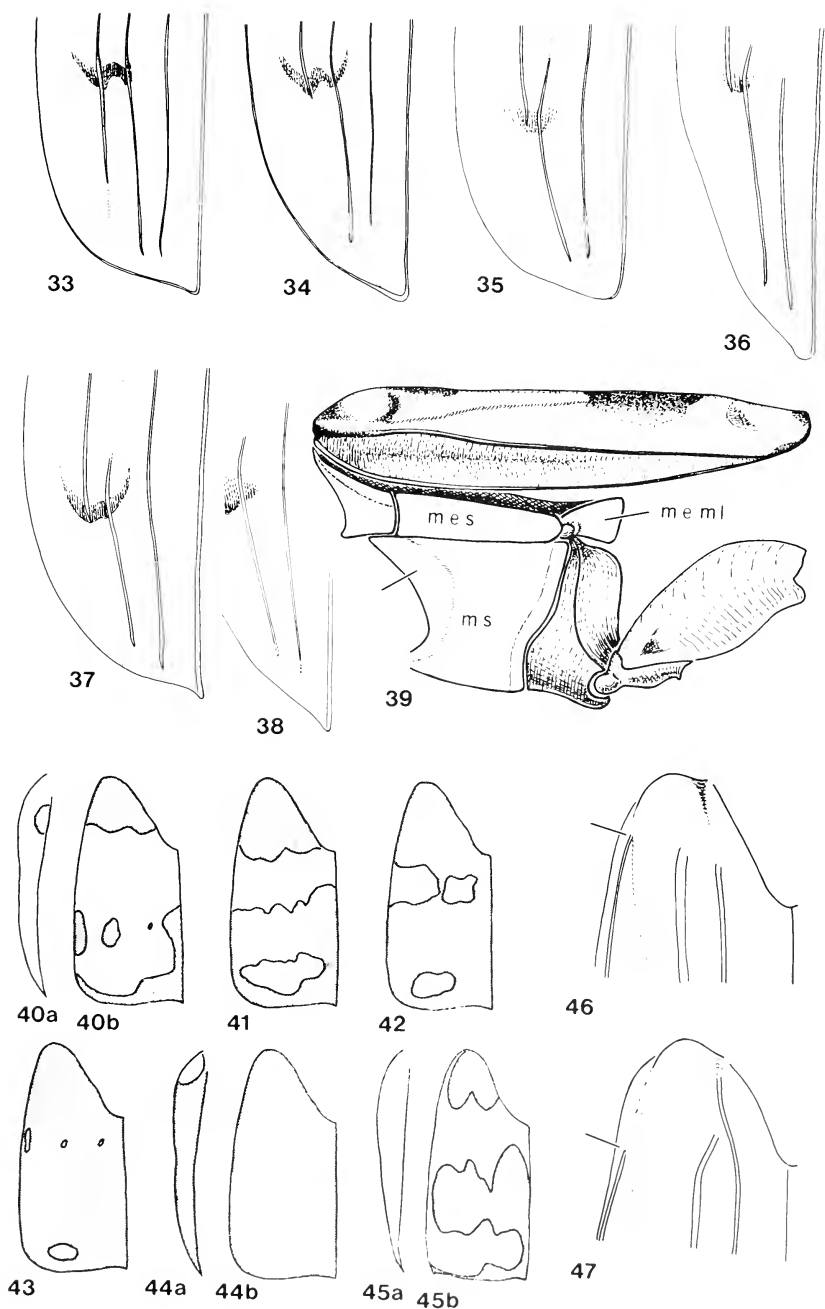


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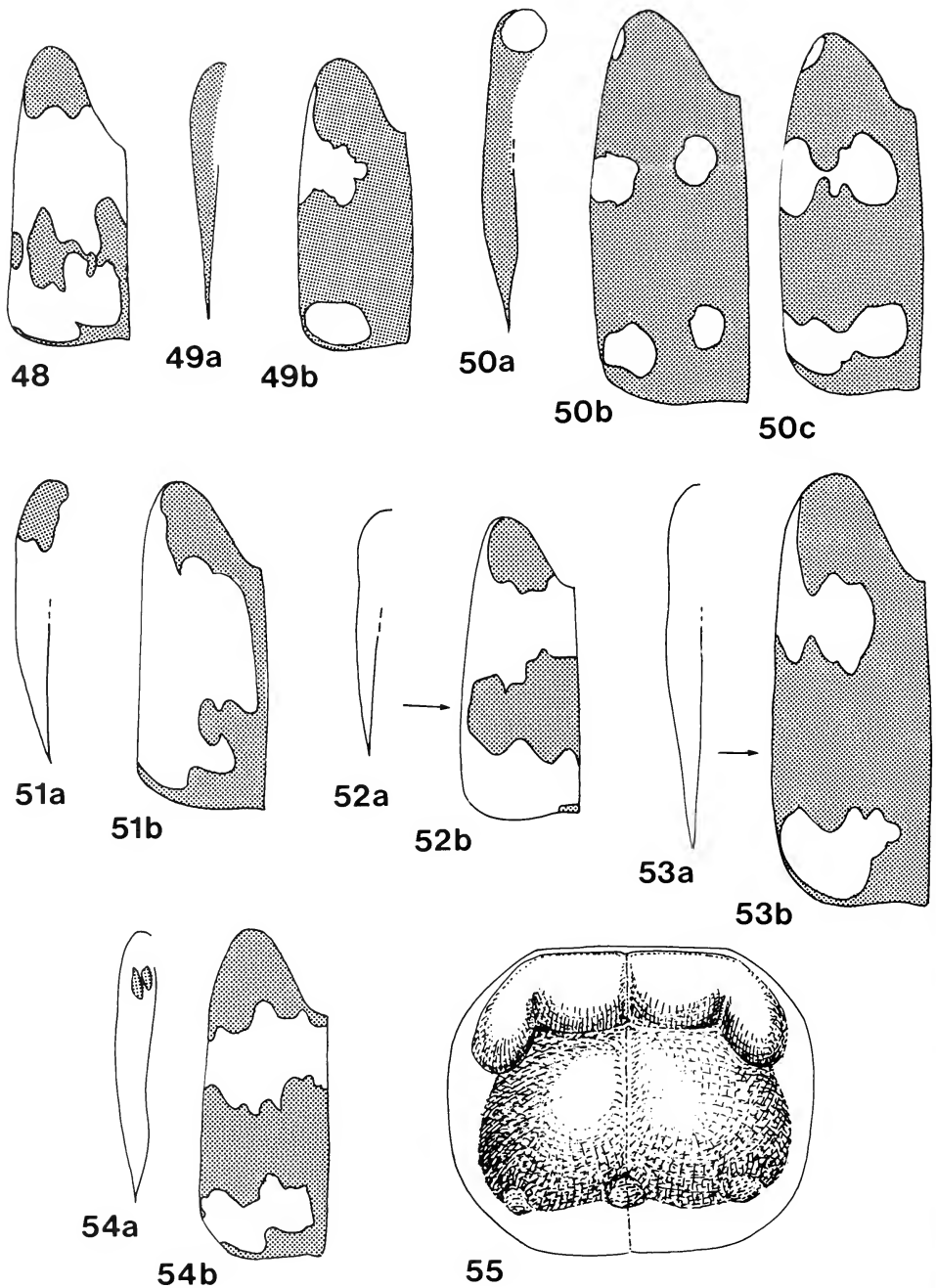


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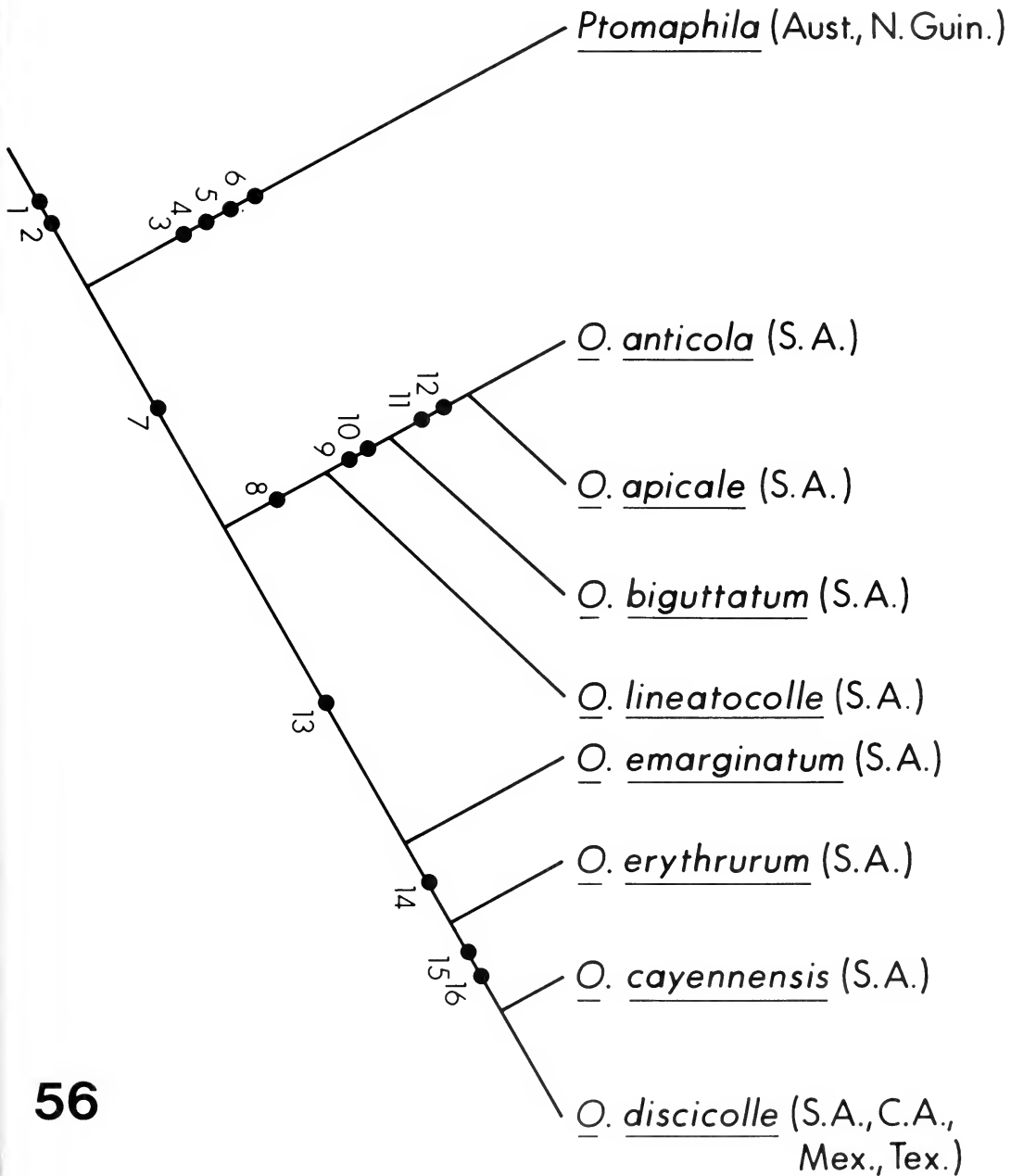
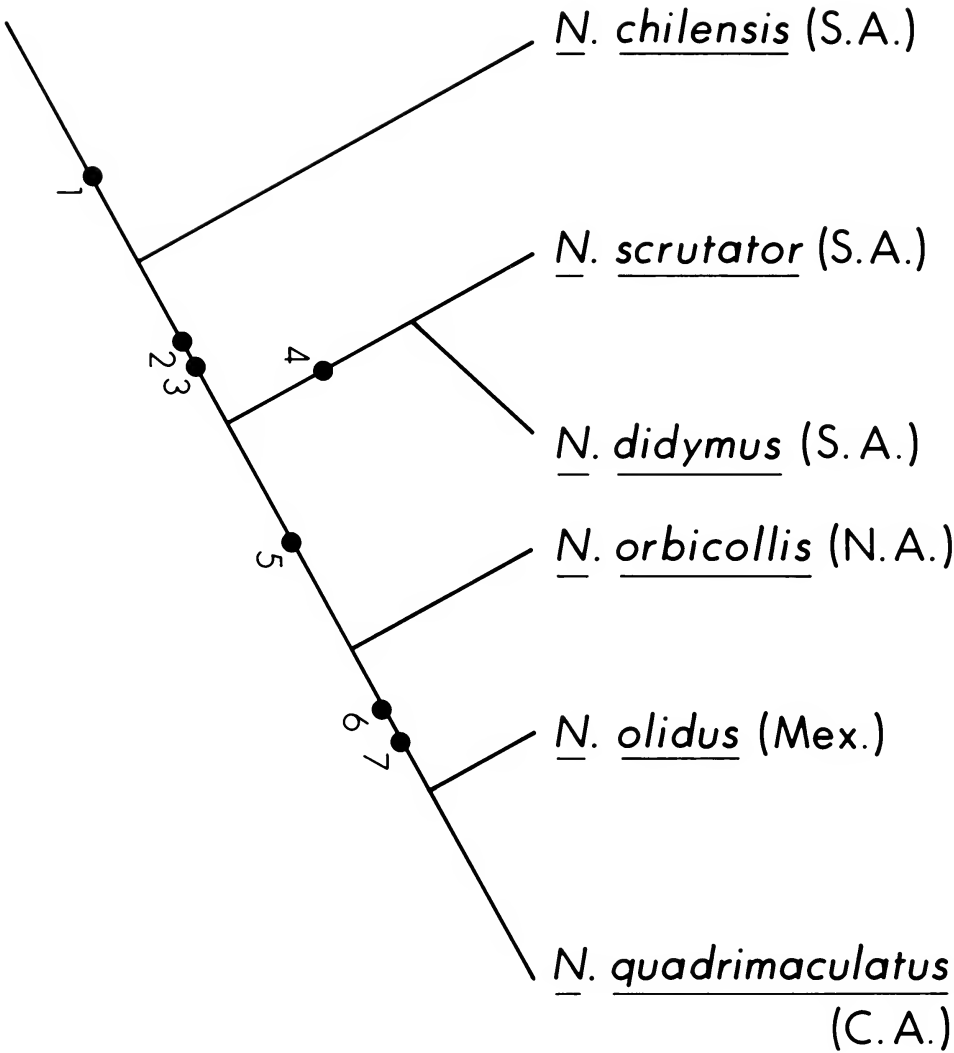


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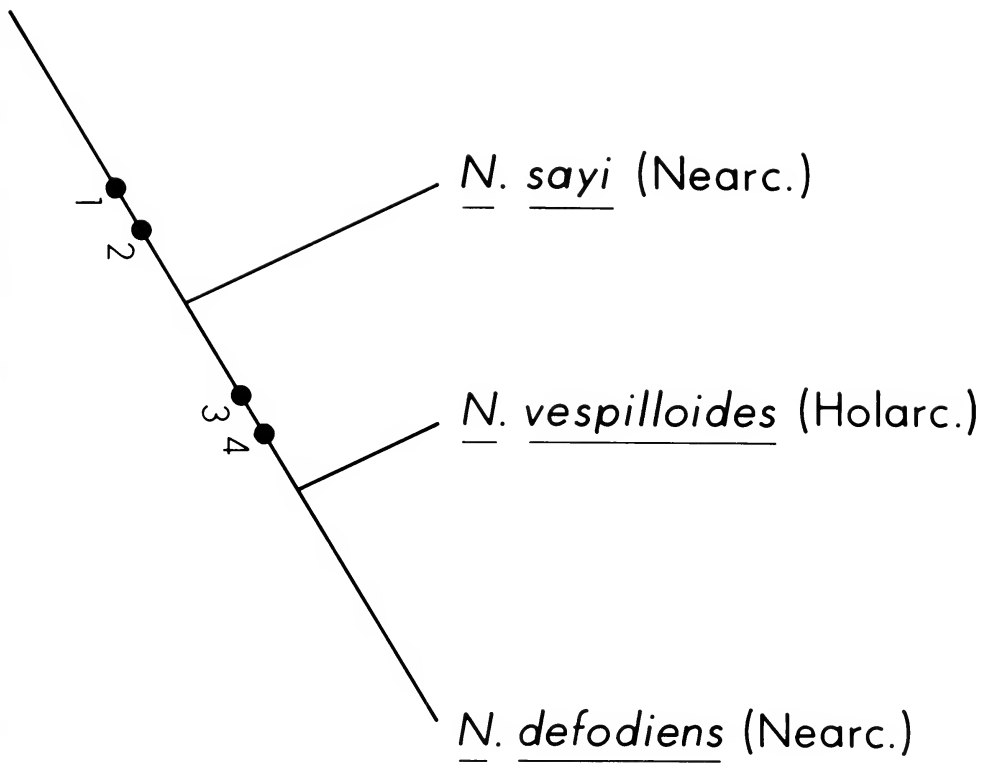
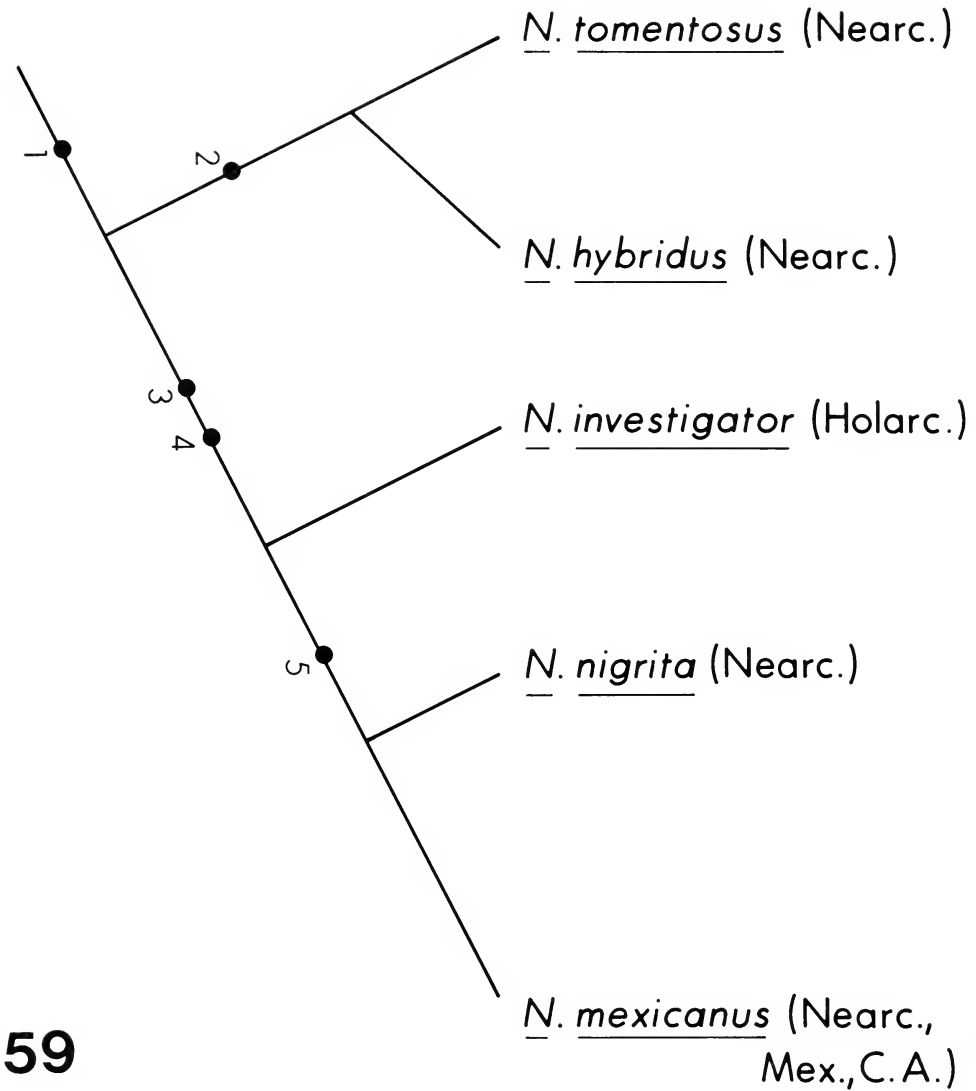
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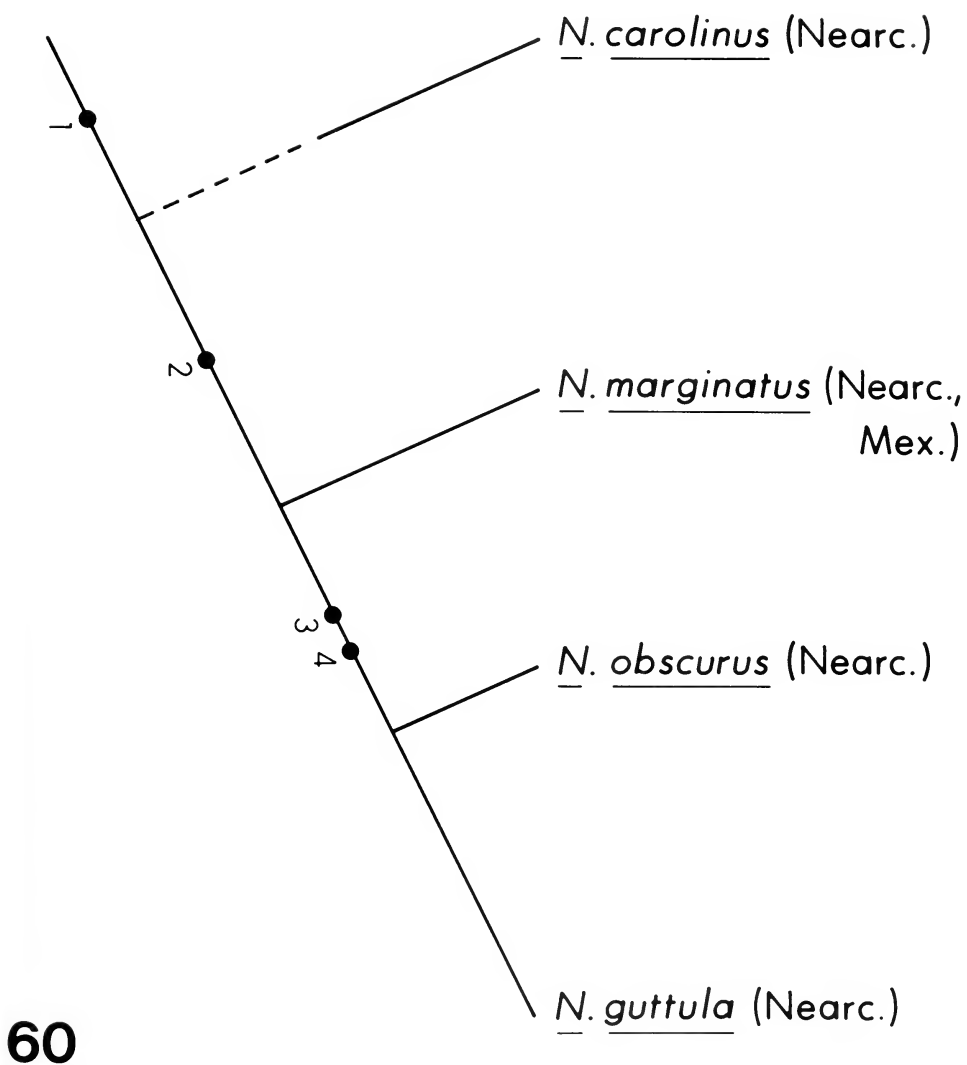
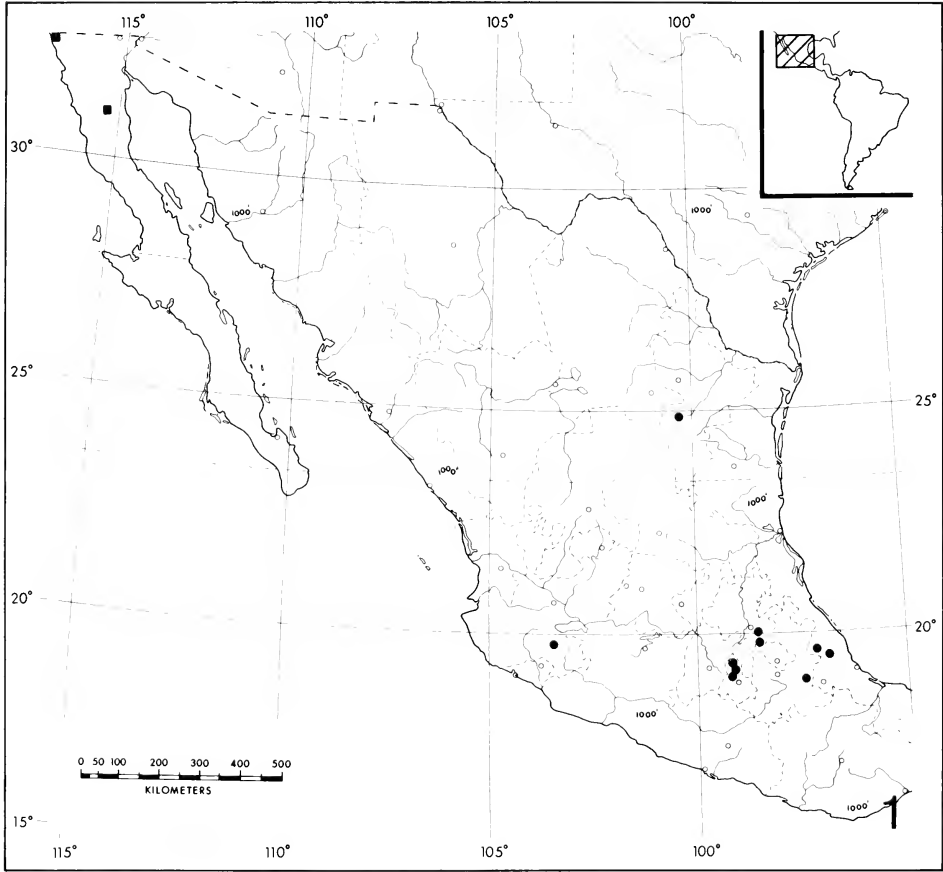
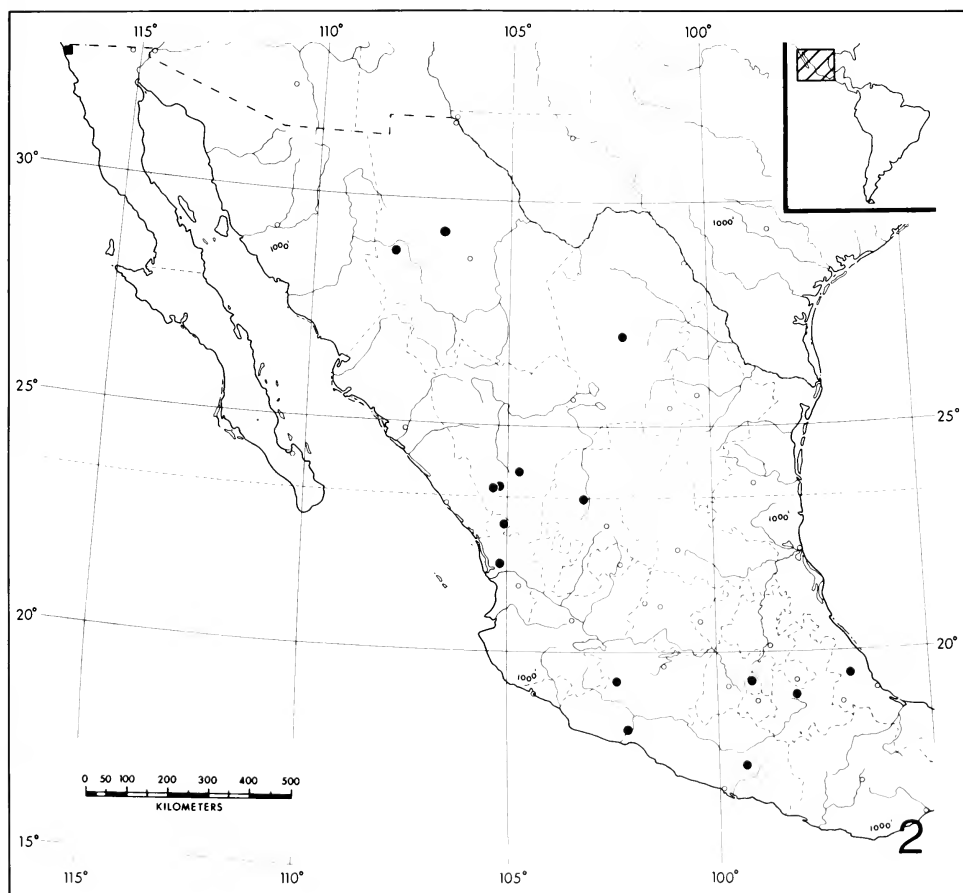


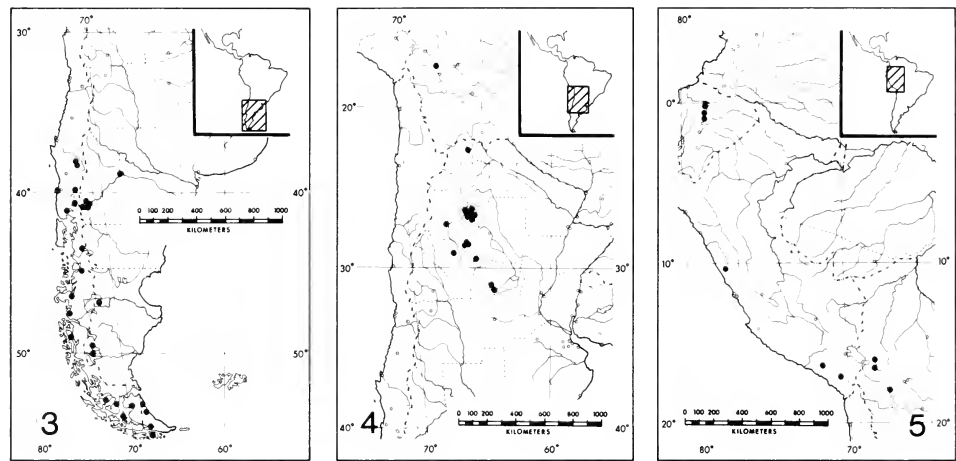
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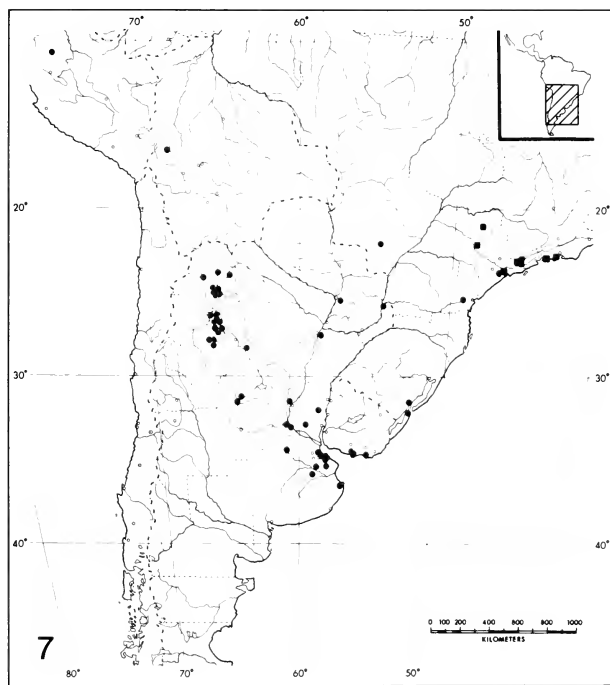
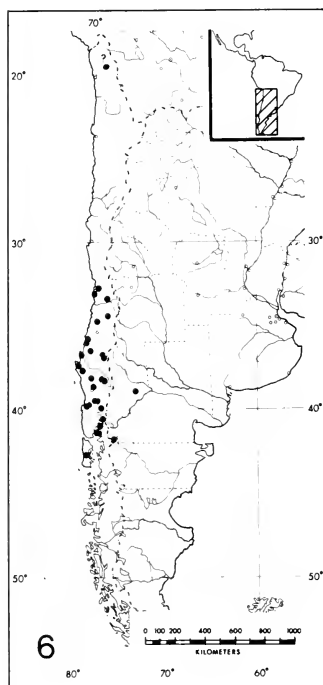
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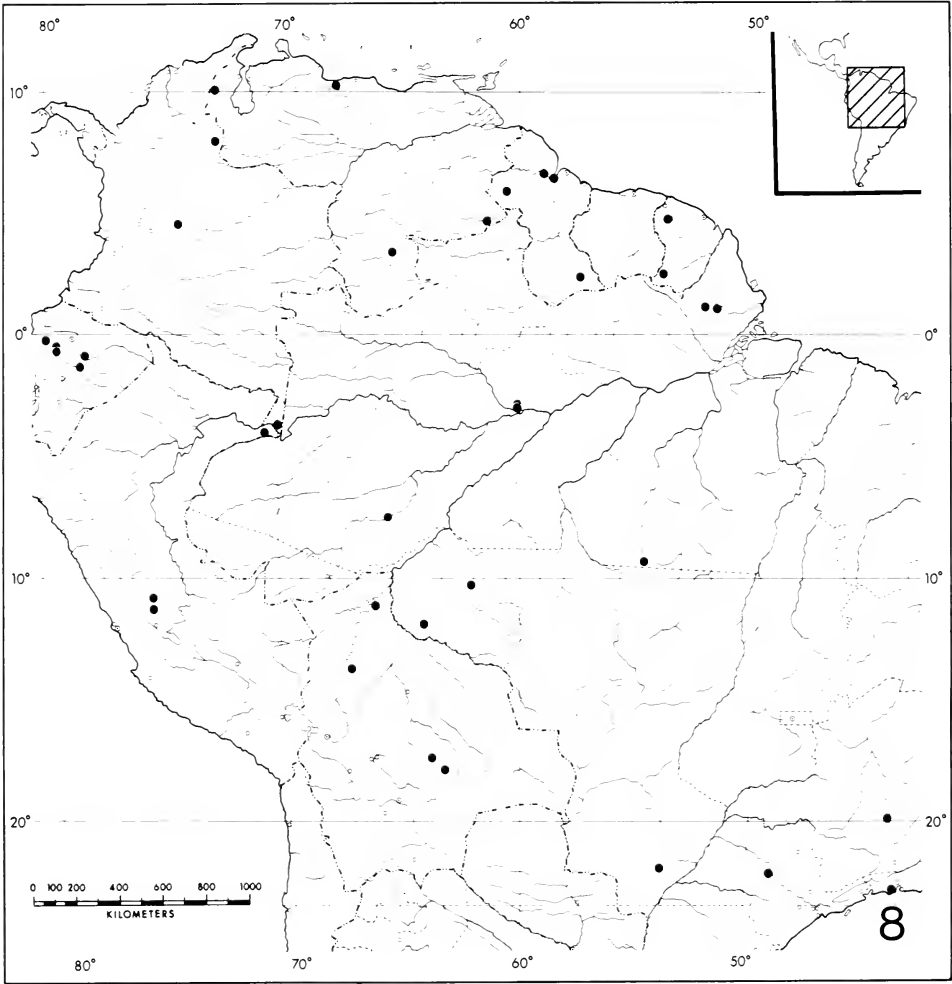
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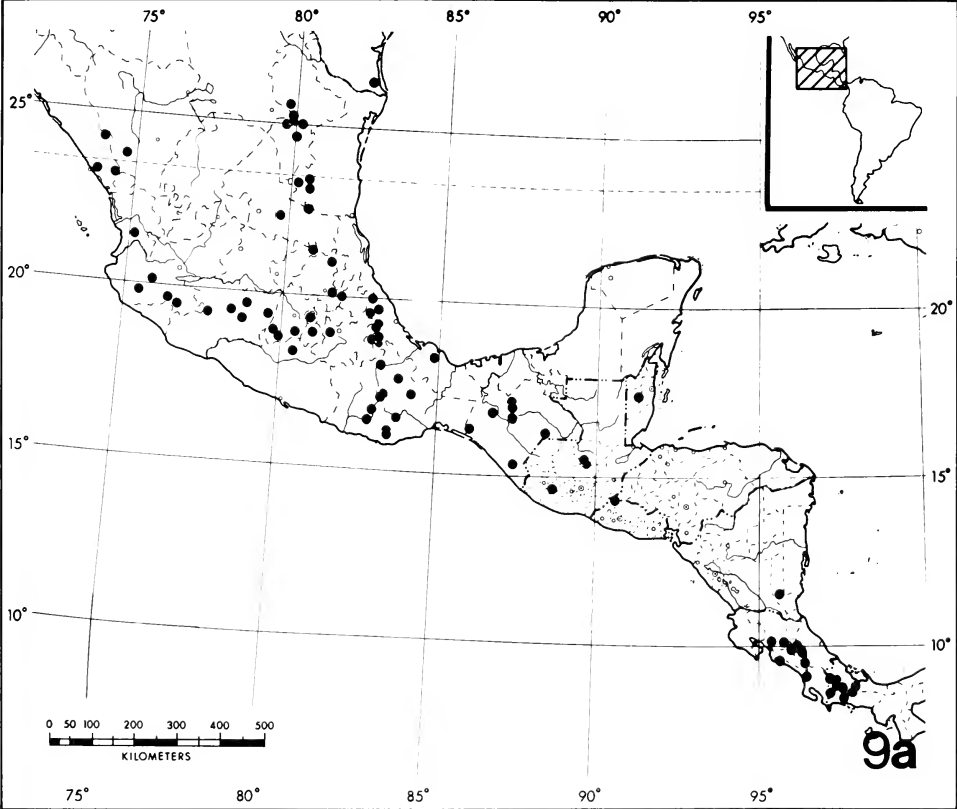
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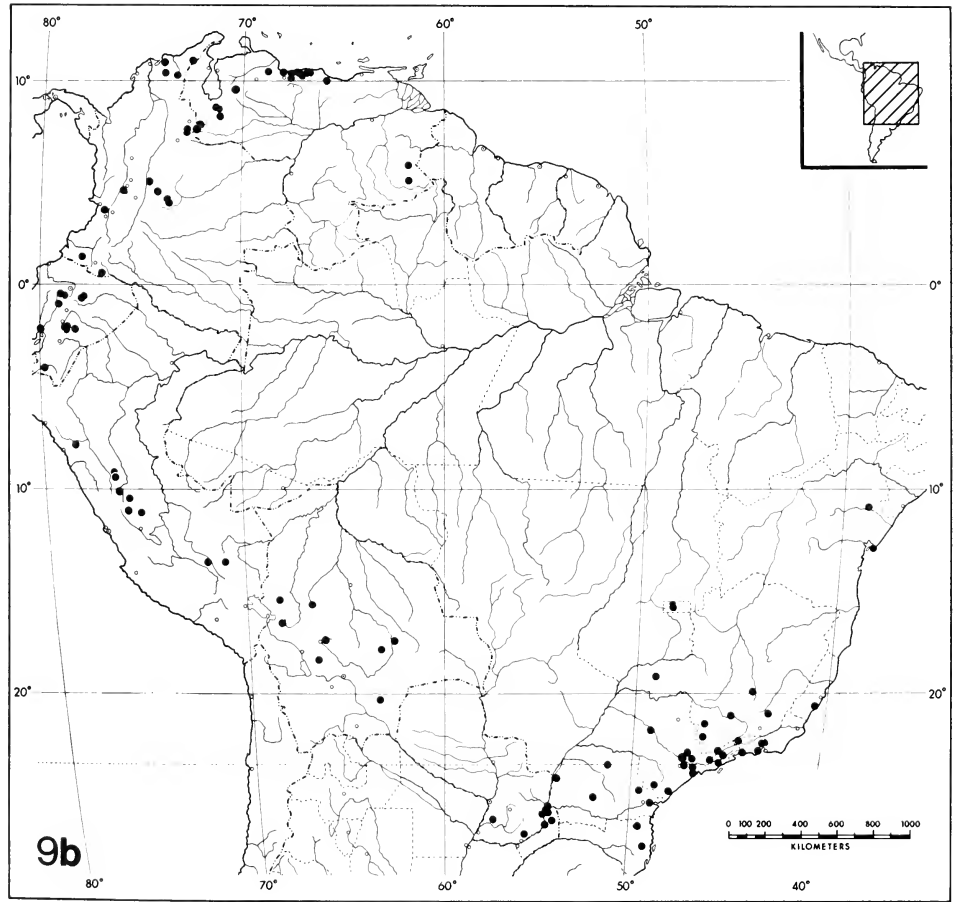
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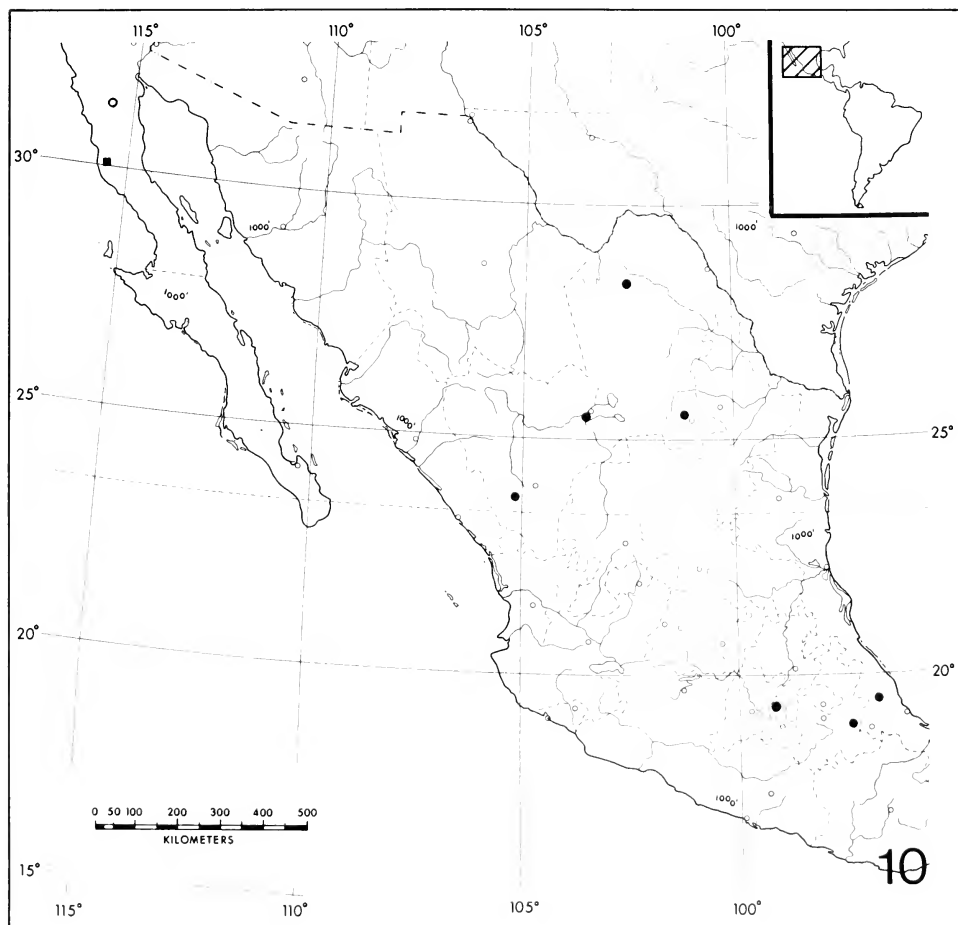
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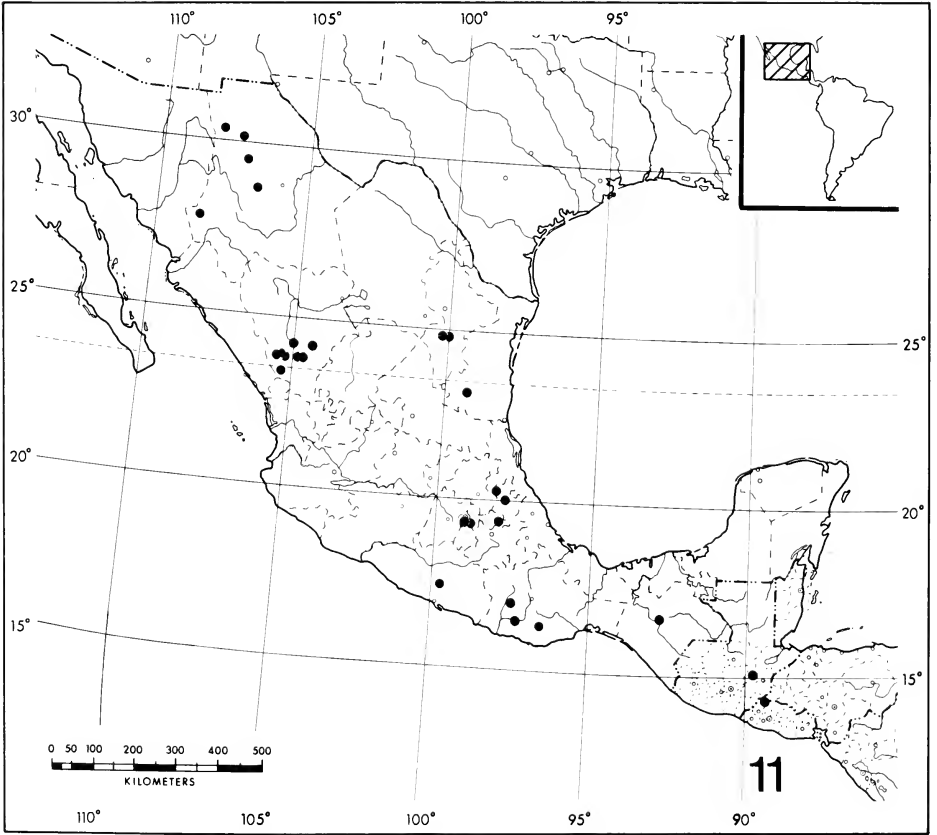
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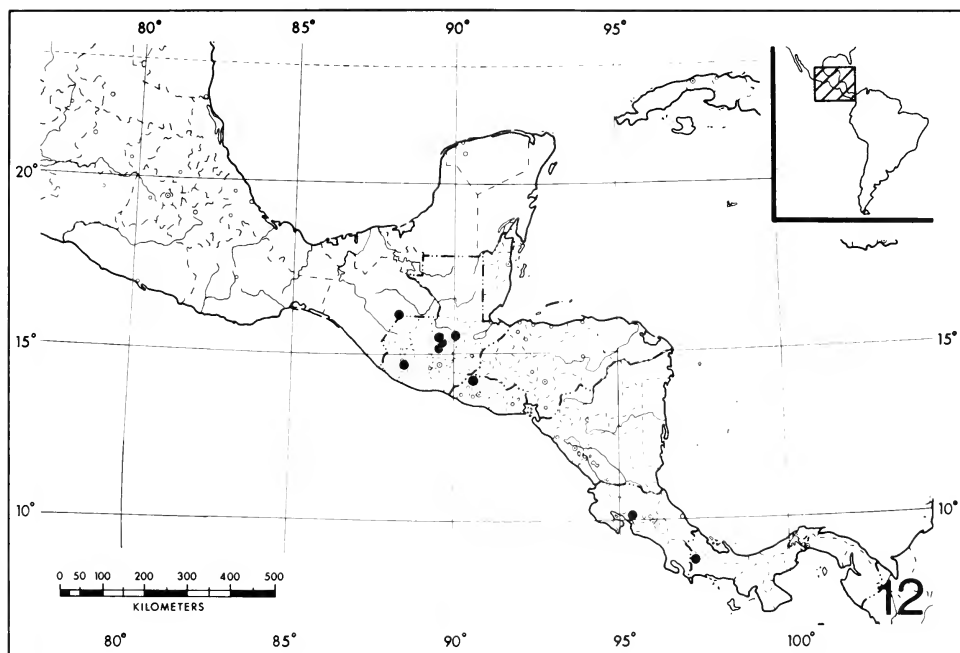
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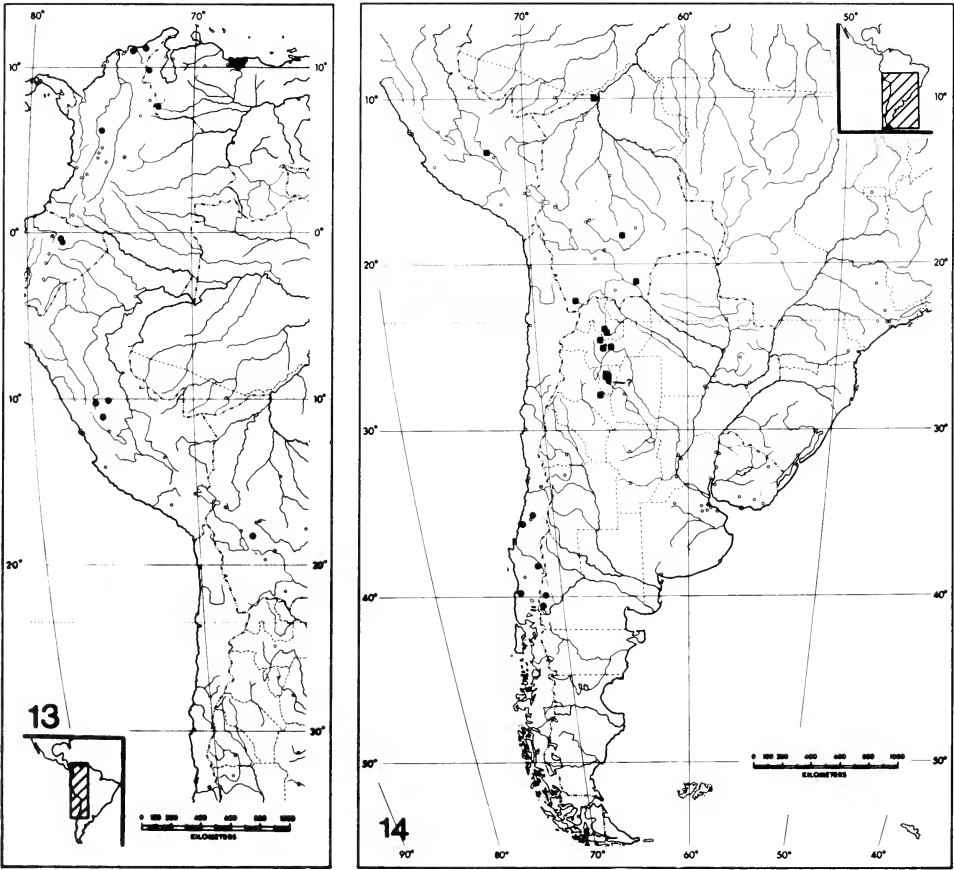
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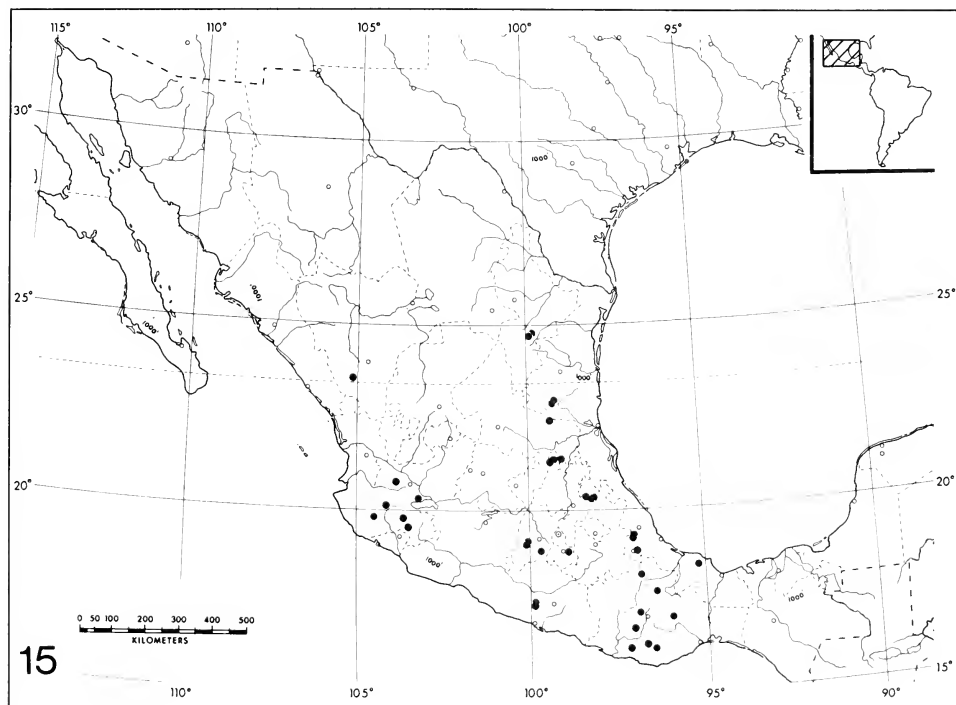
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THE TIGER BEETLES OF ALBERTA (COLEOPTERA: CARABIDAE, CICINDELINI)¹

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ABSTRACT

In Alberta there are 19 species of tiger beetles (*Cicindela*). These are found in a wide variety of habitats from sand dunes and riverbanks to construction sites. Each species has a unique distribution resulting from complex interactions of adult site selection, life history, competition, predation and historical factors. Post-pleistocene dispersal of tiger beetles into Alberta came predominantly from the south with a few species entering Alberta from the north and west.

INTRODUCTION

Wallis (1961) recognized 26 species of *Cicindela* in Canada, of which 19 occur in Alberta. Most species of tiger beetle in North America are polytypic but, in Alberta most are represented by a single subspecies. Two species are represented each by two subspecies and two others hybridize and might better be described as a single species with distinct subspecies. When a single subspecies is present in the province morphs normally attributed to other subspecies may also be present, in which case the most common morph (over 80% of a population) is used for subspecies designation.

Tiger beetles have always been popular with collectors. Bright colours and quick flight make these beetles a sporting and delightful challenge to collect.

The purpose of this paper is to provide a guide to the tiger beetles occurring in the province of Alberta. Information on life history, species recognition, habitat preference, collecting sites and a brief synopsis of biogeographical considerations for interpretation of present distribution patterns have been included.

LIFE HISTORY

Adults

Tiger beetles are capable fliers and quick on their legs, being able to escape rapidly when disturbed. Most tiger beetles are diurnal, preferring bright sun, but, some are active at night. Adults of one species in Alberta, *Cicindela lepida*, are normally active during the day, but, on warm nights, they will resume hunting activities shortly after sunset. Most tiger beetles at the onset of night or inclement weather dig shallow burrows for refuge.

Alberta *Cicindela* can also be divided into two categories based on the life span of the adult: those species having long lived adults which overwinter (spring-fall) and those in which adults

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live for a single summer (summer). In spring-fall species, adults freshly emerged from pupae prepare for winter in late summer or early autumn by excavating a deep burrow. Wintering quarters vary in depth, depending on the species and the nature of the soil. *Cicindela repanda* adults for example will dig burrows 15 to 21 cm deep in clay soils and up to 56 cm deep in sandy soils, while those of *C. formosa* have been recorded digging burrows down to 109 cm in sand (Criddle 1907).

Spring-fall-adults are sexually immature in the fall (Willis 1967) and appear to need winter chilling to break reproductive diapause. Wintered adults lay eggs the following spring.

Summer-adults do not diapause and are reproductively active within days of emerging from the pupa.

Tiger beetles can be grouped ecologically. In Alberta, adults of species found along streams tend to have dark elytra with well defined maculations (*C. repanda*, *C. hirticollis*, *C. duodecimguttata*, *C. oregona*), those found on dark soils often have reduced maculation and are black (*C. nebraskana*, *C. purpurea purpurea*, *C. longilabris*), those found along margins of sand dunes tend to be brightly coloured (*C. formosa formosa*, *C. lengi*, *C. scutellaris*) and those found in the open on drifting sand are very pale and blend in with the sand (*C. limbata nympha*, *C. lepida*, *C. formosa gibsoni*).

Food for adults consists of other insects. Almost any insect will be taken with the exception of certain bugs and of prey too large or small to handle. Large tiger beetles will prey opportunistically on members of other smaller species.

There are few effective predators of tiger beetles. Dragon flies and robber flies have been observed catching tiger beetles in flight (Graves 1962, Lavingne 1972) and birds occasionally prey on them. For example, droppings of Ringbilled Gulls (at Gull Lake, Alberta) contained pieces of elytra from *C. repanda* *C. hirticollis* (personal observation, 1973). Normally the quick movements, rapid flight and cryptic colouration of tiger beetles make their capture by people and other predators difficult.

Eggs and Larvae

Eggs are deposited in spring through summer, depending on species. The female makes a small hole in the ground with her ovipositor and deposits a single egg. The egg hatches a few weeks later into a first instar larva. This larva first enlarges its hole and then positions its head and thorax at the burrow entrance and waits for its first meal (Fig. 1). If prey is readily available, feeding will last for a few weeks, then the larva plugs its burrow entrance and remains dormant until late summer. Feeding then resumes for a few weeks or until the onset of cold weather. The larva diapauses until spring at which time feeding resumes (Hamilton 1925, Willis 1967).

Depending on the species, larvae may reach maturity (third instar), pupate and emerge as adults by the end of June (summer-adult species). Alternatively, larvae may stop feeding during mid-summer, resume feeding in late summer, then pupate and emerge as adults in late August or early September (spring-fall-adult species). In all species at least one larval instar passes through winter, but only in spring-fall species do adults survive a winter (Criddle 1907, 1910, Hamilton 1925, Shelford 1908, Willis 1967).

Tiger beetle larvae, like adults, are carnivorous. Large mandibles provide an effective means of subduing prey (Fig. 2). Larvae of *C. formosa* may dig a pit at the burrow entrance, that may be used to trap ants and other small insects (Criddle 1910). Larvae of most species do not dig a trap but lunge and seize prey near the burrow entrance. Prey is pulled into the burrow and the

larva then consumes it in relative safety. Strong abdominal spines anchor the larva to the burrow wall (Fig. 1) preventing accidental dislodgement by large prey. If the prey is too large, the larva releases the would be victim and retreats by dropping to safety at the bottom of its burrow.

Larval burrows vary in depth according to species, soil type and larval age. Depths range from a few cm for larvae of *Cicindela repanda* and *C. duodecimguttata* along stream margins to depths in excess of 3 m for those of *C. lepida* and *C. formosa* on sand dunes.

Few predators attack tiger beetle larva. Some Beeflies (*Anthrax* spp., Bombiliidae) lay eggs near burrow entrances. The hatching fly maggot may then locate and parasitize the tiger beetle larva. Parasitized larvae fail to complete development, dying during or just before pupation. Swan (1975) found up to 7% of a population of *Cicindela scutellaris* larvae to be parasitized.

Other larval parasites are members of the tiphiid wasp genus *Methocha* Latreille. These small wingless wasps wander in areas occupied by tiger beetle larvae. When siezed, the wasp immediately stings the beetle larva in the soft gular cuticle under its head, causing temporary paralysis; an egg is then deposited and the wasp wanders off to be grabbed by another victim. The narrow, elongate shape and armored cuticle of the wasp prevents it from being pierced by the larva's mandibles and allow the wasp to manoeuvre and sting the larva. The wasp larva hatches and remains attached as an external parasitoid. When the host larva pupates, the wasp larva then begins to actively feed, consuming and killing the pupa from inside out.

Pupae

Pupation occurs in a specially prepared chamber opening into the side of the larval burrow. In summer-adult species, the larvae feed in spring before molting into pupae. The larvae of spring-fall adult species feed for an extended period in the spring and may feed in late summer before molting into pupae (August). Pupation lasts for a few weeks. Summer-adult species emerge as adults in late June and early July, while spring-fall-adult species emerge as adults in late August through early September. The spring-fall-adults feed for a short time before entering winter diapause, with breeding occurring the following spring.

Possible factors influencing selection for summer or spring-fall species

Maintenance of summer and spring-fall species involves a combination of past- and presently acting selective pressures. Habitat, an obvious feature, may at first glance be implicated as a factor influencing life history. However, the four summer species in Alberta occupy different habitats. Members of *C. lepida* live on sand dunes, those of *C. nevadica* on alkaline soil, those of *C. punctulata* on gravelly prairie soil and those of *C. terricola* on clay or dark loamy grassland soils. Similar diversity of habitats are found in spring-fall species.

Interactions between tiger beetle species appear important. Interspecific contact may involve competitive interactions for adult hunting sites, food, larval burrow sites, oviposition sites, wintering sites and predation on or by other tiger beetles. For example, the spring-fall species, *C. formosa*, *C. lengi*, *C. scutellaris* and *C. limbata nympha*, and the summer species, *C. lepida* adults share overlapping habitat on the Empress sand dunes of Alberta. Habitat partitioning appears to be expressed as adult hunting sites. Food selection is similar for all species, the beetles feed on any insect of suitable size (see Willis (1967) for diet of saline habitat tiger beetles). Adults of *C. lengi*, *C. lepida* and *C. scutellaris* live in the margins of sand dunes and adjacent grasslands, while those of *C. l. nympha* live in the margins and out onto open sand. Beetles of *C. l. nympha* appear to reduce detrimental interaction (predation) by moving away

from dune margins when tiger beetles of other species are present. Temporal partitioning of habitat also effectively reduces intraspecific interactions for beetles of *C. lepida*. Adults of *C. lepida* occupy the same habitat as those of *C. l. nympha*, but at a different time of year, mid July versus May, June and August. This temporal isolation effectively removes these beetles from direct competition for food and predation with larger spring-fall tiger beetles. In regions south of Alberta, several summer species may occur in similar habitats. When this occurs additional temporal shifts may occur in population abundance (Willis, 1967).

The other, summer-adult species in Alberta do not appear to have as complex interactions with other tiger beetle species as does *C. lepida*. It is possible that being a summer-adult species has supplied a competitive advantage to members of the species either in the past or in a portion of the species present range. Following post pleistocene dispersal, these interactions may no longer occur in Alberta.

There must also be some advantage to be gained from being a spring-fall species. Upon examining distribution maps, one notices immediately that spring-fall species have ranges which extend north into cooler climatic zones. Prolonged larval development with a long feeding period allows for greater success in obtaining adequate nutrition for completion of development. In some spring-fall species, larvae may take several seasons to complete development. Interactions between other tiger beetle species are limited with one or two species occupying similar but not identical habitats.

Each tiger beetle species has its own unique history. Variations do occur, however, with some species not fitting neatly into a defined pattern. Further investigations are required to elucidate precisely what factors are involved in maintaining these two life history types in Alberta.

KEY TO THE TIGER BEETLES OF ALBERTA

This key is adapted from Wallis (1961), Freitag (1965) and Willis (1968). When two subspecies are present in Alberta, information regarding their separate recognition is included. See Fig. 3 for details on nomenclature of elytral maculation. When examining for characters such as presence of microserrations, a magnification of 40X may be required. Most of the other characters can be seen with the unaided eye or with a 10X hand lens.

- | | | |
|-------|---|---|
| 1 | Frons glabrous or with two supraorbital setae (Fig. 6) | 2 |
| 1' | Head covered with hairs or with clusters of hair on the inner margin of each eye (Fig. 5) | 6 |
| 2 (1) | Elytral apices serrate with a row of blue or green foveae (Fig. 31) | |
| | <i>C. punctulata</i> , p. 331 | |
| 2' | Elytra apices not serrulate, without a row of metallic blue to green foveae | 3 |
| 3 (2) | Small beetles, less than 15 mm, labrum short (length parallel to long axis of body less than one half its width) | 4 |
| | <i>C. terricola</i> | |
| | Larger beetles, greater than 15 mm, labrum long | 5 |
| 4 (3) | Marginal band complete (Fig. 25) | <i>C. terricola cinctipennis</i> , p. 332 |
| 4' | Marginal band reduced (Fig. 26) | <i>C. terricola imperfecta</i> , p. 332 |
| 5 (4) | Elytra shallowly punctate or sculptured into waves, shiny between punctures or on crests of waves, abdominal sternites dull black (Fig. 9) .. | |
| | <i>C. nebraskana</i> , p. 328 | |

- 5' Elytra granulate, dull or with slight sheen near base, abdominal sternites metallic green to violet (Fig. 10) *C. longilabris*, p. 327
- 6 (1) Head more or less hairy (Fig. 4), at least a few hairs on frons, if abraded punctures mark former location of hair 7
- 6' Head with only clusters of hair on anterior inner margin of each eye (Fig. 5) 20
- 7 (6) Hair on head, thorax and abdomen decumbent 8
- 7' Hair more or less erect on at least part of body (beetles killed in liquid may have matted hair), markings usually well defined 11
- 8 (7) Dark elytral markings not sharply defined, legs pale, on sand dunes (Fig. 32) *C. lepida*, p. 333
- 8' Dark elytral markings more sharply defined, legs dark 9
- 9 (8) Elytral dark markings reduced, mostly pale (Fig. 13) *C. limbata nympha*, p. 326
- 9' Elytral dark markings not greatly reduced, more typical banding pattern 10
- 10 (9) Middle band straight and oblique, not "hooked" at end, pale markings heavy, wide (Fig. 12) *C. limbata hyperborea*, p. 326
- 10' Middle band sinuous, curved, hooked at end, pale markings not heavy; alkali washes (Fig. 30) *C. nevadica*, p. 332
- 11 (7) Marginal line joined or touching humeral lunule 12
- 11' Marginal line separated, not touching humeral lunule, often greatly reduced 15
- 12 (11) Humeral lunule "c" shaped 13
- 12' Humeral lunule oblique, pale markings wide 14
- 13 (12) Genae glabrous (Fig. 7), posterior tip of humeral lunule (when present) with slight anterior hook (marginal line may touch apical lunule, Fig. 11) *C. hirticollis*, p. 326
- 13' Genae setose (if hairs abraded, punctures mark their former position, Fig. 8), marginal line usually separated from apical lunule (Fig. 14) *C. repanda*, p. 324
- 14 (12) Length greater than 15 mm, line of humeral lunule obliterated totally or in part by marginal band (Figs. 21 & 22) *C. formosa*, p. 328
- 14' Length less than 15 mm, humeral lunule long, spur may almost touch middle band (Fig. 23) *C. lengi*, p. 330
- 15 (11) Marginal line greatly reduced or absent, humeral lunule absent or reduced to spots (Figs. 27, 28 & 29) 16
- 15' Marginal line present (Figs. 18, 19 & 20), obvious spur, humeral lunule present 18
- 16 (15) Middle band wide long, apical end not markedly curved, color green to violet (Fig. 28) *C. decemnotata*, p. 329
- 16' Elytral markings thin, light, middle band more strongly curved, shorter than width of elytron 17
- 17 (16) Post humeral spot usually absent, middle band widely separated from margin, color green or black (Fig. 27) *C. purpurea*, p. 328
- 17' Post humeral spot usually present, middle band narrowly separated or touching margin, color red or greenish, middle band transverse, often

- strongly curved at apical end (Fig. 29) *C. splendida limbalis*, p. 329
- 18 (15) Genae glabrous (Fig. 7), elytra with greasy appearance, pale markings heavy, on alkali soils and washes (Fig. 20) *C. fulgida*, p. 330
- 18' Genae with hairs or or setigerous punctures (Fig. 8) 19
- 19 (18) Humeral lunule "c" shaped, scape (basal segment) of antenna with few hairs (Fig. 18) *C. duodecimguttata*, p. 325
- 19' Humeral lunule oblique, scape of antenna hairy (more than 10 hairs) (Fig. 19) *C. tranquebarica*, p. 331
- 20 (7) Elytra not serrulate, non punctate, in Alberta red/green elytra without pale maculations (Fig. 24) *C. scutellaris*, p. 330
- 20' Elytra punctate, serrulate, color brown, blue, olive, maculations typical to reduced *C. oregona* 21
- 21 (20) Pleura of thorax blue/purple, elytra brown, green, blue, maculations narrow, pronotum brown (Fig. 15) *C. oregona oregona*, p. 325
- 21' Thoracic pleura coppery, elytra dark brown, maculations narrow (Fig. 16) *C. oregona guttifera*, p. 325

TIGER BEETLES OF ALBERTA

1. *Cicindela repanda* Dejean (Figs. 14 & 33)

C. repanda repanda Dejean

Recognition.— (Fig. 14) These beetles resemble members of *C. duodecimguttata*. Separation between them is based on configuration of the marginal band: in *C. repanda* the band is continuous or narrowly separated from the humeral lunule (Fig. 14), whereas in *C. duodecimguttata* the band has a wide gap (Fig. 18). For positive identification the male genitalia must be examined (see Freitag (1965) for method). *Cicindela duodecimguttata*, *C. repanda*, *C. hirticollis*, *C. limbata* and *C. oregona* form part of the Maritima group and many species in this group resemble each other.

Habitat.— These beetles inhabit sand, gravel and clay soils with sparse vegetation adjacent to streams and rivers. Adults may be found running near the water over patches of mud. Wintering grounds for the adults may be some distance from their summer haunts. Winter burrows are made in bare dry hillsides (Criddle 1907). Larvae may be found scattered through vegetation near stream or pond margins. This species has a two year life cycle, with the third instar larva passing through the first winter and the adult the second (Hamilton 1925).

Localities.— (Fig. 33) Athabasca River (5 km east, Chain Lakes), Barker Lake, Barrier Reservoir, Brazeau River (near Lodgepole), Calgary, Chin (4.8 km south), Crimson Lake, Clyde (6.5 km east), Deadwood (banks of Peace River), Devon, Dilberry, Drayton Valley, Dunvegan, Edmonton, Empress (11 km south), Fawcett, Flatbush (Pembina River), Fort MacKay, Fort McMurray, Garth, Gem, Gibbons, Green Island (sic!, =Verte Island), Gull Lake, House River, Jenner, Lesser Slave Lake, Little Smoky River, Lethbridge, Medicine Hat, McGrath, Meikle River (Mackenzie Highway), Milk River (junction with Lost River), North Saskatchewan River (near Rocky Mountain House), Patricia (near), Peace River, Pembina River (near Lodgepole), Red Deer, Red Deer River (near Bindloss), Saunders, Smoky River, Wainwright, Wapiti River (south of Grande Prairie).

2. *Cicindela duodecimguttata* Dejean (Figs. 8, 18 & 34)

Recognition.— (Figs. 8 & 18) This species is similar to *C. repanda* but is more closely related to *C. oregona* and hybridizes with it along the Rocky Mountain Foothills of Alberta (Freitag, 1965). Populations of *C. duodecimguttata* occur east of the foothills and populations of *C. oregona* to the west along mountain valleys. Hybrid populations have markings intermediate to those of *C. oregona* and *C. duodecimguttata* (Freitag 1965) (Fig. 17). The humeral lunule may be narrowly broken or expressed as a spot and the marginal line is of variable length.

Habitat.— These beetles live close to pond and stream margins. When in association with *C. repanda*, beetles of *C. duodecimguttata* move away from the water's edge reducing habitat overlap. Adults and larvae winter in burrows 1.2 to 2 m back from the stream or pond margin. If the water rises in spring before beetles are active, large numbers may perish (Criddle 1907). Members of this species have a two year life cycle similar to that of *C. duodecimguttata*.

Localities.— (Fig. 34) Andrew, Beaverhill Lake, Bilby, Brazeau River (near Lodgepole), Calgary, Chin, Clyde (6.5 km east), Cooking Lake, Crimson Lake, Cypress Hills, Doussal, Drayton Valley, Edmonton, Fallea, Flatbush, Fort Chipewyan, Fort McMurray, Fort MacKay, Gull Lake, Happy Valley (Porcupine Hills), Halfwayhouse, Jenner, Lake Cardinal, Lesser Slave Lake, Lethbridge, Louis Bull Reservation, Medicine Hat, North Saskatchewan River (near Rocky Mountain House), Police Lake, Redwater, Saunders, Smith-Fitzgerald Road (km 11), Stirling Lake, Tilley, Tofield, Vilna, Wabamum.

3. *Cicindela oregona* LeConte (Figs. 15, 16 & 35)

C. oregona oregona LeConte (Fig. 15)

C. oregona guttifera LeConte (Fig. 16)

Recognition.— (Figs. 15 & 16) These beetles are distinguished from those of related species by the presence of small groups of hairs on the inner margin of each eye. Markings are similar to those of *C. duodecimguttata* and *C. repanda*. This species hybridizes with *C. duodecimguttata* in the foothill region (Freitag 1965) (see discussion under *C. duodecimguttata*) and in the Northwest Territories.

Wallis (1961) called the Albertan populations *C. oregona guttifera*. On examination of Albertan material I found these beetles to be intermediate between *C. oregona oregona* and *C. oregona guttifera* which agrees with Freitag (1965). Members of the subspecies *guttifera* are characterized by a humeral lobe represented by two large spots, the dorsal surface is more or less olive with a metallic lustre, thoracic pleura are coppery and the ventral surface is bicolored. The elytral spine is small and serrulations of the apex are weak. Representatives of the subspecies *oregona* are similar to *guttifera* but the elytral spine and serrulations are well developed and the thoracic pleura are metallic blue like the ventral surface. Imprecise definition of Albertan populations is due to hybridization of *C. o. oregona* with *C. o. guttifera* and *C. duodecimguttata*. The specimen collected in the Peace River area was clearly *C. o. guttifera*.

Habitat.— Individuals of *Cicindela oregona* live along margins of streams and lakes on clay or sandy soils with little vegetation cover. The habitat may be shared with members of *C. repanda*, *C. duodecimguttata*, and *C. hirticollis*.

Localities.— (Fig. 35) *C. o. oregona* X *C. o. guttifera*: Athabasca Falls, Banff, Carbondale, Castle River, Highwood River, Hillcrest, Kootenay Plains, Laggan (=Lake Louise), New Dayton (1.6 km east), North Saskatchewan River (near Nordegg), Waterton.

C. o. guttifera: Green Island (sic!, = Verte Island).

4. *Cicindela hirticollis* Say (Figs. 11 & 36)

Recognition.— (Fig. 11) Members of this species are distinguished from others of the Maritima group by the strongly "C" shaped humeral lunule on the elytra. In other respects they are similar to members of *C. repanda*.

C. hirticollis is represented by one form throughout most of Canada. Subspecies recognition is based on width of elytral maculations. Most specimens have wide markings and are called *C. h. ponderosa* Thoms. The problem is that, within local populations, many individuals may have narrow maculations and could be assigned to another subspecies. Dull brown elytra are the norm, but, on the Athabasca drainage, some blue beetles have been collected. Due to the wide geographic range and nature of variation I do not feel that assigning the Albertan populations to a particular subspecies is appropriate.

Habitat.— These tiger beetles are found on light colored beach sands with little or no vegetation. The habitat may be shared with other members of the Maritima group. This species appears to have summer-adults.

Localities.— (Fig. 36) Athabasca River, Calgary, Crimson Lake, Dunvegan, Empress, Fort McMurray, Gull Lake, Jasper, Jasper Lake, Lac La Biche, Lesser Slave Lake, Medicine Hat, Red Deer, Red Deer River (near Bindloss), Snaring River (Jasper National Park).

5. *Cicindela limbata* Say (Figs. 4, 12, 13, 37 & 38)

Cicindela limbata nympha Casey (Figs. 4, 12 & 37)

Cicindela limbata hyperborea LeConte (Figs. 13 & 38)

Recognition.— (Figs. 4, 12 & 13) Two subspecies, very different in appearance, occur in Alberta.

Individuals of *Cicindela limbata nympha* are distinguished by the pale elytra with reduced dark markings. The marginal band is expanded to cover most of the elytra leaving a narrow dark band down the centre. A brownband identifies the subspecies *nympha*, a green band *C. l. limbata*. Nearly all of the specimens examined were marked with the brown; hence the Albertan populations are assigned to *C. l. nympha*.

Specimens of *Cicindela limbata hyperborea* do not look like those of the southern subspecies. Instead they resemble other members of the Maritima group of which *C. limbata* is a member. Markings are of typical tiger beetle design with a brown elytral ground color. The greatly thickened elytral bands distinguish members of this subspecies from those of all other Maritima group species found in Alberta.

Habitat.— These beetles prefer sandy blowouts or sand dunes which are sparsely vegetated. When the species is present it is usually very abundant. Adults are known to winter in loose sand. Beetles of *Cicindela limbata nympha* occur on prairie sand dunes and blowouts, whereas those of *C. l. hyperborea* are found in similar habitats in the boreal forest. Individuals of the northern subspecies also occur in disturbed sandy areas along roadways. In Manitoba *C. l. nympha* has a three year life cycle (Criddle 1907, Hamilton 1925).

Localities.— *C. l. nympha*: (Fig. 37) Blindman River, Bruderheim, Calgary, Chauvin, Claysmore, Clyde, Clyde (6.5 km east), Crimson Lake, Czar, Dilberry, Egerton, Edmonton, Empress, Empress (11 km south), Gull Lake, Hondo, Lesser Slave Lake, Nestow, Orion, Opal, Pakowki Lake, Ponoka (5 km south), Red Deer, Ribstone, Rochester, Stauffer, Tawatinaw, Winterburn.

C. l. hyperborea: (Fig. 38) Barber Lake, Fort Chipewyan, Fort MacKay, Fort MacKay (10 km south), Fort Mackay (8.5 km east, north of Athabasca River Bridge), Fort McMurray, Fort Smith (N.W.T., northern border of Alberta), Gregorie Lake.

6. *Cicindela longilabris* Say (Figs. 10 & 39)

Cicindela longilabris longilabris Say

Recognition.— (Fig. 10) This tiger beetle of the foothill and boreal regions is closely related to *C. nebraskana*. Correct identification is often difficult. Species determination is based on microstructure of the elytra and habitat preference when known.

Adults of are characterized by smooth or very slightly waved sculpture on the elytra. The surface is covered with minute granules giving the beetle a dull lustre. If shiny areas do occur, these are small and restricted to the crests of the waves. The lustre may be due to wear on the elytra in older beetles.

Cicindela nebraskana adults have a larger shiny area, giving the elytra more lustre. A series of granulate punctures surrounded by a glossy mesh or well developed series of waves and ridges are characteristic of this species. Members of *Cicindela nebraskana* live in prairie grasslands and of *C. longilabris* in forest clearings and meadows.

In the Alberta foothills, prairie grassland extends along valley bottoms and on southwest-facing hill sides into the mountains in several places (e.g. Bow River Valley, Crowsnest Valley). In these areas the ranges of these two species overlap. Hybridization has not been observed to occur between them. In localities of overlap, they appear to partition the habitat. Individuals of *Cicindela longilabris* stay near clearings on sandy soils with conifer trees and of *C. nebraskana* on clay soils of the valley grasslands.

Hatch (1953) did not recognize *C. montana* LeConte (= *C. nebraskana*) as a valid species but rather as a variation (abberation) of *C. longilabris*. My experience with these species indicates that they are morphologically very similar but can be distinguished and that they have different habitat preferences. Populations of *C. longilabris* in Alberta are composed primarily of black beetles, with slender feeble markings, hence assignment to the subspecies *C. longilabris longilabris*. However, there are individuals of other phenotypes present. Beetles with heavy markings and a bronzed color are of the *laurenti* Schaupp phenotype, and those with slender markings with a vivid green are of the *perviridis* Schaupp phenotype.

Habitat.— *Cicindela longilabris* adults prefer sandy areas such as ridges and blowouts in conifer forests. Adults are found along sandy forest paths and road sides, and over winter.

Localities.— (Fig. 39) Banff, Barber Lake, Barrier Reservoir, Beaverlodge, Beauvallon, Calling River Ranger Station, Canmore, Cline River, Crimson Lake, Coleman, Crowsnest Lake, Drayton Valley, Edmonton, Exshaw, Fairview (10 km southeast), Fedora, Fortress Mountain, Fort MacKay, Fort MacKay (8.5 km east, north of Athabasca River Bridge), Fort McMurray (22.4 km north), George Lake, Gorge Creek, Green Island (sic!, = Verte Island), Hargwen, Hinton, Kananaskis Lakes, Kootenay Plains, Marlboro, Millarville, North Saskatchewan River (near Nordegg), Opal, Peace River, Pembina River (near Fawcett), Poachers Landing (Tp.69 Rge.19 W.4), Prairie Bluff Mountain, Robb, Rocky Mountain House, Sand Hill Lake, Saunders, Waterton, Wapiti River (south of Grande Prairie), Whirlpool River, Winterburn.

7. *Cicindela nebraskana* LeConte (Figs. 6, 9 & 40)

Cicindela nebraskana nebraskana LeConte

Recognition.— (Fig 6 & 9) Adults of this species are slightly smaller than those of *C. longilabris* and have reduced elytral maculations. Ground color of the elytra is black to slightly bronzed. Features for separating specimens of *C. nebraskana* from those of *C. longilabris* are discussed under *C. longilabris*.

The Alberta subspecies is *C. nebraskana nebraskana*. Many subspecific names have been created to describe minor differences in various populations. In Alberta the beetles examined were within the normal range of variation for the subspecies *nebraskana*. These are smooth black to slightly bronzed beetles from prairie grasslands.

Habitat.— These beetles prefer open bare areas between clumps of grass and earth mounds made by ground squirrels. *Cicindela nebraskana* occurs throughout the prairie grasslands on heavy clay soils, and overwinter as adults.

Localities.— (Fig. 40) Barrier Reservoir, Calgary, Carbondale River (junction of Lost Creek), Chin (5 km south), Coronation, Del Bonita, Dorothy, Drumheller, Evans-Thomas Creek, Empress (11 km south), Exshaw, Kananaskis River (Ribbon Creek), Frank, Gorge Creek, Ghost Dam, Highwood River, Hilda, Jenner, Lethbridge, Manyberries, Medicine Hat, Milk River (16 km north of Aden), Milk River (junction with Lost River), Oyen (4.8 km south), Pincher, Porcupine Hills, Prairie Bluff Mountain, Scandia, Seebe, Strathmore, Standard, Stettler, Steveston, Taber.

8. *Cicindela formosa* Say (Figs. 21 & 41)

Cicindela formosa formosa Say

Recognition.— (Fig. 21) This is the largest of the Albertan tiger beetles. The shape of the humeral lunule is distinctive. Superficially, adults of *C. formosa* resemble adults of *C. lengi*. In Alberta the species is represented by the typical subspecies *C. formosa formosa*. Adults have a bright metallic lustre on the ventral surface, with the pigmented areas of the elytra red to red-purple.

Another subspecies, *C. formosa gibsoni* Brown (Figs. 22 & 42), occurs a few kilometers east of the Alberta boundary, in the Great Sand Hills of Saskatchewan. Characteristics of these beetles are: a metallic venter and reduced elytral pigmentation with the marginal band expanded to cover most of the elytra. This subspecies should be watched for in sandy areas near the Saskatchewan boundary.

Habitat.— Beetles of *Cicindela formosa* inhabit sandy blowouts and marginal areas of active sand dunes in areas of sparse vegetation. Adults spend the winter in deep burrows dug into the side of sand dunes. The beetles are sometimes slow to appear in spring because of the slow warming of deeper sand.

Localities.— (Fig. 41) Empress, Empress (11 km south), Fort Macleod, Gem, Medicine Hat, Sandy Point, South Saskatchewan River (junction with Red Deer River).

9. *Cicindela purpurea* LeConte (Figs. 27 & 43)

Cicindela purpurea purpurea X *C. p. auduboni* LeConte

Recognition.— (Fig. 27) Beetles of this species come in two color forms, black or green. In Alberta most specimens lack the subhumeral spot, and this readily distinguishes them from adults of *C. splendida limbalis*

The name *C. purpurea purpurea* refers to populations of black beetles, and *C. purpurea auduboni* to populations of green beetles. Populations in Alberta are similar to those across the Great Plains, being comprised of a mixture of green and black beetles. Subspecies designation is normally written as *C. p. purpurea X auduboni* to reflect the mixture of forms. The subspecies in Alberta is *C. p. purpurea X auduboni*.

Habitat.— These beetles are found on patches of bare clay soil interspersed with clumps of grass and other plants. This habitat occurs frequently in prairie grasslands. *Cicindela purpurea* winters as an adult. Members of this spring-fall species require at least two years for larval development.

Localities.— (Fig. 43) Aden, Bassano, Brooks, Burdett, Calgary, Castor, Cessford, Cypress Hills, Dillberry, Edmonton, Empress (11 km south), Etzikom, Fort Macleod, Ghost River, Gleichen, Hanna, Hussar, Jenner, Lethbridge, Lost River (5 km north, junction with Milk River), Magrath, Manyberries, Medicine Hat, Merid, Milk River, Orion, Pincher Creek, Ross Creek, Taber, Tilly, Walling.

10. *Cicindela splendida* Hentz (Figs. 29 & 44)

Cicindela splendida limbalis Klug

Recognition.— (Fig. 29) Elytral maculations of these beetles are similar to those of adult *C. purpurea*. The reddish tinge and presence of a subhumeral spot on the elytra serve as distinguishing features. Wallis (1961) considered *limbalis* as a separate species, without distinct forms. Johnson (in prep.) includes *limbalis* as a subspecies of *Cicindela splendida*. Beetles of the *limbalis* phenotype are characterized by a coppery to brown head and prothorax with moderately wide elytral maculations. The *denverensis* phenotype is characterized by blue-green colors and more variable elytral maculations. In Alberta, beetles with coppery greenish to coppery brown colors occur. Johnson considers these beetles to be a blend of *limbalis* and *denverensis* phenotypes. The majority of specimens in Alberta can be assigned to the *limbalis* phenotype, hence the subspecies designation, *C. splendida limbalis*.

Habitat.— These beetles prefer steep clay banks for breeding purposes but adults may be found almost anywhere. I have collected them in the reedy margin of a slough in Calgary. The usual habitat is on bare clay banks of streams. These beetles have a two year life cycle with overwintering adults.

Localities.— (Fig. 44) Bilby, Brocket, Calgary, Calling River Ranger Station, Devon, Edmonton, Elk Island National Park, Fairview, Fawcett, Fort MacKay, Fort McMurray, Fox Creek, George Lake, Gleichen, Golden Spike, Grande Prairie, Happy Valley (Porcupine Hills), Heatherdown, Lausand, Leduc, Nestow, Nevis, Pembina River, Pincher, Pincher Creek, Pouce Coupe (B.C., east in Alberta), Prairie Bluff Mountain, Red Deer, Redwater, Stauffer, Smoky Lake, Stettler, Sundance, Trochu, Wabamum, Wapiti River (south of Grande Prairie), Wetaskwin.

11. *Cicindela decemnotata* Klug (Figs. 28 & 45)

Recognition.— (Fig. 28) This green or violaceous tiger beetle is characterized by reduction of the humeral lunule and a long, descending arm of the middle band of the elytron. There are no recognized subspecies.

Notes.— The violet form of this species is common in the Peace River district and a population of this beetle occurs in grasslands surrounding Whitehorse, Yukon Territory. Adults of this species should be watched for in grassland areas along northern rivers.

Habitat.— These beetles occur on clay, sandy, or gravel soils often along cowpaths and roads. Adults are frequently captured on clay alluvium in badlands and are known to overwinter.

Localities.— (Fig. 45) Deadwood, Dorothy, Drumheller, Empress (11 km south), Fairview (16 km southeast), Fort Macleod, Green Island (sic!, = Verte Island), Happy Valley (Porcupine Hills), Lethbridge, Lost River (5 km north, junction with Milk River), Manyberries (8 km south), Manyberries (32 km south), Majestic, Medicine Hat, Milk River (junction with Lost River), Onefour, Peace River, Pincher, Taber.

12. *Cicindela fulgida* Say (Figs. 7, 20 & 46)

Cicindela fulgida fulgida Say

Recognition.— (Figs. 7 & 20) These beetles differ from all other Albertan cicindelids in their heavy maculation pattern and greasy appearance. Adults of the subspecies *C. fulgida fulgida* are 12 mm in length and have a brilliant coppery to coppery green lustre. The humeral lunule is widely separated from the middle band at its tip.

Habitat.— Members of this species occur on alkaline soils along streams, badlands, coulees and some sloughs on the prairies. Adults are found in areas devoid of vegetation. Beetles can be collected early in spring and late in fall, implying a wintering adult.

Localities.— (Fig. 46) Chappice Lake, Grassy Lake (2.5 km south), Jenner Ferry (now Jenner Bridge), Onefour, Lost River, Medicine Hat, Sandy Point.

13. *Cicindela scutellaris* Say (Figs. 5, 24 & 47)

Cicindela scutellaris scutellaris Say

Recognition.— (Figs. 5 & 24) Adults of this species cannot be mistaken for those of any other species of Albertan tiger beetle. Bright red elytra lacking all maculations characterize this species in Alberta. Subspecies recognition is also based on absence of maculations and on bright red color; other subspecies have reduced maculations along the elytral margins.

Habitat.— Beetles of *Cicindela scutellaris* occur on blowouts and sand dunes in southern Alberta and inhabit the sparsely vegetated edge zone dominated by Scurf Pea (*Psorealea lanceolata* Pursh). The sand dune habitat is shared in part with representatives of *Cicindela formosa*, *C. lengi* and *C. limbata nympha*. Adults overwinter.

Localities.— (Fig. 47) Chappice Lake, Drumheller, Empress, Empress (11 km south), Medicine Hat.

14. *Cicindela lengi* Horn (Figs. 23 & 48)

Cicindela lengi versuta Casey

Recognition.— (Fig. 23) Adults of this species appear similar to those of *Cicindela formosa* but are distinguished by their smaller size, and long, straight humeral lunule. Most Albertan specimens have a reddish elytral ground color. A few beetles examined were green and one was bright metallic blue. Since the majority of specimens have reddish elytra and coppery thoracic sclerites the subspecific name *C. l. versuta* applies. The name *C. l. lengi* refers to blue to blue-green populations. Other color variations also occur; a deep purple specimen was taken at Opal and Wallis (1961) reported a black specimen from Saskatchewan.

Habitat.— Members of this species inhabit dry open sandy areas in the grasslands of Alberta and may be found on prairie sand dunes and boreal forest sand ridges. These spring-fall beetles may take up to three years to complete larval development. Adults winter in burrows

dug in sandy soil.

Localities.— (Fig. 48) Barber Lake, Blackfalds, Chappice Lake, Claysmore, Clyde (6.5 km east), Edgerton, Edmonton, Empress, Empress (11 km south), Fort Macleod, Milk River (16 km north of Aden), Milk River (junction of Lost River), Opal, Pakowki Lake, Rolling Hills, Sand Hill Lake, Writing on Stone Provincial Park (32 km east).

15. *Cicindela tranquebarica* Herbst (Figs. 19 & 49)

Cicindela tranquebarica kirbyi LeConte

Recognition.— (Fig. 19) The long, obliquely-directed, descending arm of the humeral lunule is a distinguishing character. *Cicindela tranquebarica* is common and widespread.

Geographical variation in *C. tranquebarica* is complex and poorly known. Many names have been given to local varieties. The dominant phenotype found in Alberta is that of *C. t. kirbyi* LeConte. The markings are broad with a bronzy-green ground color. North of Alberta, adults of *C. t. borealis* Harrington, can be recognized by a broken humeral lunule band or by the ends of the band narrowly joined in the middle. I have not seen material from Alberta representing the *borealis* phenotype. However specimens from north of Wandering River had reduced band widths although further north, at Fort MacKay, elytral band widths reverted back to the wide state. Specimens of *Cicindela tranquebarica borealis* should be watched for in northern Alberta.

Habitat.— Representatives of this species occur in almost any tiger beetle habitat, ranging from alkaline mud flats, sandy blowouts, and prairie grasslands to boreal forest trails. Disturbed areas are readily colonized. Areas with reduced vegetation cover are preferred. These beetles overwinter as adults.

Localities.— (Fig. 49) Aden (16 km west), Barber Lake, Barnwell, Barons, Bilby, Brazeau River (near Lodgepole), Calgary, Calling Lake Ranger Station, Castor, Chappice Lake, Chin, Claresholm, Clyde (6.5 km east), Clyde (10 km north), Clymont, Consort, Crimson Lake, Deadwood, Drayton Valley, Drumheller, Dunvegan, Edmonton, Empress (11 km south), Fairview (16 km southeast), Fawcett, Fort MacKay, Fort Macleod, Fort McMurray (22.4 km north), Garth, Golden Spike, Gorge Creek, Grande Prairie, Gull Lake, High River, Jenner, Jenner Ferry (Jenner Bridge), Kootenay Plains, Lac La Biche, Lake Cardinal, Lethbridge, Lethbridge (8 km south), Lesser Slave Lake, Lundbreck, Medicine Hat, Milk River (junction of Lost River), Nanton, Nestow, New Dayton (1.6 km east), North Saskatchewan River (near Nordegg), Opal, Peace River, Pincher, Police Lake, Ranfurly, Red Deer, Rosedale, Sand Hill Lake, Smoky River, Snaring River (Jasper National Park), Saint Mary's Reservoir, Simpson, Soda Lake, Stavely, Stauffer, Tofield, Vilna, Wandering River (64 km north), Wetaskiwin, Winterburn, Writing on Stone Provincial Park (32 km east).

16. *Cicindela punctulata* Oliver (Figs. 31 & 50)

Cicindela punctulata punctulata Oliver

Recognition.— (Fig. 31) Adults of *Cicindela punctulata* are readily distinguished by a row of metallic blue or green dots running down the length of each elytron. The other elytral maculations are quite variable, ranging from immaculate to well marked. Usually the maculations consist of a few white spots. *Cicindela punctulata punctulata* is the only known subspecies occurring in Canada.

Habitat.— *Cicindela punctulata* occurs in the southern prairie regions. Thin grass with bare patches of sandy loam is preferred. Adults survive a single summer with the larvae being the

only wintering stage. Members of this species are reported to have a one year life cycle (Shelford 1908), however Hamilton (1925) speculated that it took two years to reach maturity.

Localities.— (Fig. 50) Bassano (junction of Highways 1 & 550), Burdett, Comrey, Empress (11 km south), Grassy Lake, Happy Valley (Porcupine Hills), Jenner, Lethbridge, Medicine Hat.

17. *Cicindela terricola* Say (Figs. 25, 26, 51 & 52)

Cicindela terricola cinctipennis LeConte (Figs. 25 & 51)

Cicindela terricola imperfecta LeConte (Figs. 26 & 52)

Recognition.— (Figs. 25 & 26) Adults of *Cicindela terricola cinctipennis* are small slender beetles with an unbroken marginal band. The middle band of the elytra may be distinct or reduced.

Adults of *Cicindela terricola imperfecta* are slightly larger. The marginal band is greatly reduced or at most the humeral lunule is represented by a small spur which joins up with the middle band.

Notes.— Some believe that these subspecies should be elevated to full species status. This recognition is supported by their distinct appearance, habitat preference and geographic distribution.

Cicindela terricola imperfecta ranges through British Columbia into western Alberta, on the Kootenay Plains near Nordegg. *C. oregona* (also primarily found in B.C.) is found here as well. To the west of the plains are low mountain passes into British Columbia. It appears that individuals of this subspecies dispersed eastward over the mountains along river valleys into Alberta, colonizing the grasslands of Kootenay Plains. To the east, extensive montane forest appears to have prevented further dispersal onto the prairies. Specimens of *Cicindela terricola imperfecta* should be watched for in other mountain grasslands along the foothills. It would be very informative if mixed populations of *C. t. imperfecta* and *C. t. cinctipennis* could be found. This would help in determining the species or subspecies status of the two forms.

Adults of *Cicindela terricola cinctipennis* have been taken in the grasslands around Whitehorse, Yukon Territory. This species should be watched for in all native grassland areas in Alberta.

Habitat.— Adults of *Cicindela terricola cinctipennis* prefer sparse grass on clay soils in the prairie grasslands. Wallis (1961) reported that these beetles may also be found on saline and alkaline soils with sparse vegetation. Adults of *C. t. imperfecta* have been taken on sandy clay soils on river banks, the type of habitat on which the beetles were captured at Kootenay Plains (Ball, pers. com. 1975). Adults of both subspecies are active during midsummer.

Localities.— *Cicindela terricola cinctipennis*: (Fig. 51) Calgary, Dorothy, Drumheller, Dunvegan, Empress, Fairview (16 km southeast), Fort Macleod (junction Highways 1 & 2), Green Island (sic! = Verte Island), Hussar, Jenner, Lethbridge, Manyberries, Medicine Hat, Milk River (junction of Lost River), Munson, Patricia (near), Redcliff.

Cicindela terricola imperfecta: (Fig. 52) Kootenay Plains.

18. *Cicindela nevadica* Leconte (Figs. 30 & 53)

Cicindela nevadica knausi Leng

Recognition.— (Fig. 30) These tiger beetles resemble those of *C. cuprescens*, a nonresident species. Adults of *Cicindela nevadica knausi* are bronze with off-white elytral maculations. The humeral lunule is slightly recurved toward the base and body hairs are decumbent. Only one

subspecies is known from Canada, *C. n. knausi*.

Habitat.— These beetles may be found along margins of streams and lakes on alkaline soil. Adults prefer open areas with sparse vegetation and are active during midsummer.

Localities.— (Fig. 53) Jenner Ferry (Jenner Bridge), Lost River (near junction with Milk River), Sandy Point.

19. *Cicindela lepida* Dejean (Figs. 32 & 54)

Recognition.— (Fig. 32) Adults of this species are the palest tiger beetles in Alberta and have obscure markings and pale legs offering them excellent cryptic protection on pale sand. It is often easier to see the beetle's shadow on the ground than it is to see the beetle.

Notes.— Adults of *Cicindela lepida* may become inactive when ground surface temperatures exceed 48° C during midafternoon. They burrow beneath the lethal temperature zone and resume activity when the temperature drops later in the day. On warm evenings activity will continue through the night, with short pauses at dusk and dawn. When night time temperatures exceed 25° C (rarely in Alberta), adults may disperse. In Nebraska I have collected flying adults in a black light trap many kilometers from the nearest sand dune.

Habitat.— Representatives of *Cicindela lepida* occur on pale yellow to white sand, usually on sand dunes. No vegetation or other protective cover is present. Adults prefer wind-swept dune crests and larvae are found in sheltered bowl areas on sand dunes. Members of this summer species take two years to complete their life cycle (Criddle 1910, Hamilton 1925, Shelford 1908). Adults are present from late June to early August in Alberta.

Localities.— (Fig. 54) Empress (11 km south).

Tiger beetles of the species *Cicindela lepida* occur in the Great Sandhills of Saskatchewan, just east of the Alberta boundary. Specimens should be watched for in the sand dunes and blowouts of the Middle Sand Hills of Alberta.

20. Other species.

In Vaurie's paper (1950, p 153) *Cicindela togata* La Ferté is reported to occur in Alberta. This report is a typographical error and should read *C. tranquebarica* as per species references later on the page. No additional records or specimens have been located. Wallis (1961) did not include this species as part of the Canadian tiger beetle fauna. The known range of *Cicindela togata* does not extend north of Nebraska (Willis 1967). This species is not expected to be found in Alberta.

Members of *Cicindela togata* inhabit alkali mud flats a type of habitat abundant in the south eastern corner of the province. Adults are pale with reduced pigment areas of the elytra. For details on appearance and habitat see Willis (1967).

Another species not yet recorded but to be watched for is *Cicindela cuprescens* LeConte. This species occurs in Manitoba and along the lower reaches of the Milk River in Montana. Adults are characterized by a peculiarly shaped humeral lunule, which resembles the maculations found on beetles of *C. nevadica knausi*. The strongly embossed maculations distinguish specimens of *C. cuprescens* from those of *C. n. knausi*. In Manitoba, adults of *C. cuprescens* have been collected on the sandy crest of a ravine. Willis (1967) characterized these beetles as inhabitants of fluvial mesic and saline habitats. This species may occur along the Milk River drainage in southern Alberta.

BIOGEOGRAPHIC CONSIDERATIONS

The Albertan tiger beetle fauna is of relatively recent origin. The displacement of biota by the Wisconsinian glaciation is well documented (e.g. Wright and Frey 1965, Flint 1971, Matthews, 1979, etc). Movement of biota back into glaciated regions is not as well understood.

Faunal and floral elements survived in well-identified refugia during this glaciation but which elements of the biota survived in which refugia? Workers (e.g. Ross 1970, Martin 1958, Frenzel 1973, etc.) have variously interpreted where these elements went and which factors influenced their distribution.

A poor fossil record for beetles (Morgan *et al.* 1983) necessitates the use of distribution patterns to interpret faunal source regions for Albertan tiger beetles. Modern species/subspecies distribution maps (Freitag 1965, Wallis 1961, Willis 1967) provide data on possible source regions. Source areas for Albertan tiger beetles can, potentially, be any of the following; 1) nunataks: refugia surrounded by glacial ice usually harbouring endemic forms; 2) north of the ice: unglaciated areas of Alaska and the Yukon; and 3) south of the ice: unglaciated continental North America. Region 3 can be subdivided into three major subregions, a) western: the Pacific Northwest, west of the Rocky Mountains, b) central: the Great Plains region, and c) eastern, including the boreal forest.

Tiger beetles are sensitive to low temperature and short growing season as shown by their absence from extreme northern, alpine and subalpine regions. It is therefore unlikely that any species survived on nunataks within glacial areas or in regions close to ice margins during glacial maxima.

A northern source area for Albertan tiger beetles is suggested by present distribution patterns (Fig. 56). One species, *C. oregona*, has several subspecies. Freitag (1965) showed that *C. oregona guttifera* ranges from Alaska and the Yukon through northern British Columbia. From central British Columbia and south, *C. oregona guttifera* hybridizes with *C. oregona oregona* in a zone which extends south along the Rocky Mountains into Utah. From Colorado and south into New Mexico *C. oregona guttifera* hybridizes with *C. oregona navajoensis* Van Dyke and with *C. oregona maricopa* Leng in southwest Utah. "Pure" populations of *C. oregona guttifera* occur in Colorado and New Mexico in the south and in northern British Columbia, Yukon and Alaska. These widely separated population loci and extensive zones of hybridization suggest that the ancestors of *C. oregona guttifera* were isolated in the unglaciated regions of Alaska and the Yukon in the north and in the mountainous areas of New Mexico and Colorado east of the Great Divide during the last glacial period. Populations of these beetles dispersed north and south following deglaciation whereby contact was renewed with other subspecies/sibling species. The hybrid zones reported by Freitag (1965) are these areas of contact. Thus it appears that at least one tiger beetle species may have dispersed into Alberta from a northern refugium.

The remaining tiger beetle species probably originated from source areas south of the Wisconsinian ice margin. One subspecies, *C. limbata hyperborea* may be tentatively attributed to a southeastern origin. These tiger beetles are restricted to the boreal forest in northern Alberta and Saskatchewan (Fig. 56). A problem with attributing an eastern origin to the subspecies is that there are no extant populations known from the east. Rates of subspeciation have been proposed for montane carabids (Kavanaugh 1979) but it is not known how quickly tiger beetles can subspeciate. In most tiger beetle species there is considerable individual variation. It is possible that such rates are rapid and that *C. l. hyperborea* evolved to subspecies

status while isolated on the jack pine sand plains of northern Alberta and Saskatchewan in the past 7000 years. Another explanation is that ancestral populations survived on "boreal" sand hills south of glacial ice and are now absent from these areas. Additional research is required to solve this problem.

A southwestern source region for *Cicindela terricola imperfecta* and *C. oregona oregona* (Fig. 56) is readily supported by populations found along mountain passes and valleys of western Alberta. Populations of these beetles appear to be in the process of dispersing and colonizing Alberta. Both subspecies occur in British Columbia and the U.S.A., west of the Great Divide.

The remaining Albertan tiger beetles probably originated on the central Great Plains. Populations of these species in Alberta are simply northern extensions of these ranges (Fig. 55). Habitat and climate appear to limit dispersal. Ranges of summer species do not extend north of the prairie grasslands, whereas some spring-fall species have ranges extending north into the Northwest Territories along streams and river banks (*C. splendida limbalis*, *C. tranquebarica*, *C. duodecimguttata*, *C. repanda*). A number of 'southern grassland' tiger beetle species (*C. decemnotata*, *C. lengi versuta*, and *C. terricola cinctipennis*) occur in the prairie regions of the Peace River district and two species (*C. decemnotata*, and *C. t. cinctipennis*) in the grasslands of the Yukon. This distribution parallels that of many plant species (Moss 1952).

Following deglaciation the fauna moved around, adjusting to changes in climate. About 7000 years B.P. a prolonged warm period, the hypsithermal occurred. During this time, prairie grasslands probably expanded north in Alberta at the expense of the forested regions. The grasslands of the Peace River district and the southern prairies were continuous, with a resulting exchange of floral and faunal elements. Since the hypsithermal, the climate has cooled and the forests have reclaimed much of these grasslands. This has resulted in the reduction and isolation of remnants of northern grasslands with their relict prairie flora and fauna.

Other tiger beetle species (*C. lepida*, *C. formosa*) may have dispersed north into Alberta during the hypsithermal when dune habitats were in abundance. Riparian species (*C. repanda*, *C. duodecimguttata*, *C. hirticollis*) followed the changing water sheds, losing habitat in times of drought and flood. Species of alkaline mud flats (*C. fulgida*, *C. nevadica*) would lose habitat during pluvial periods and gain it back during periods of drought. The tiger beetle fauna is thus in a constant state of flux. Some species are still colonizing the province, some are represented by relict populations, and others are adapting and flourishing in the wake of man's activities: colonizing and dispersing along roadways, and breeding in construction sites. Agriculture has destroyed some habitats and created others.

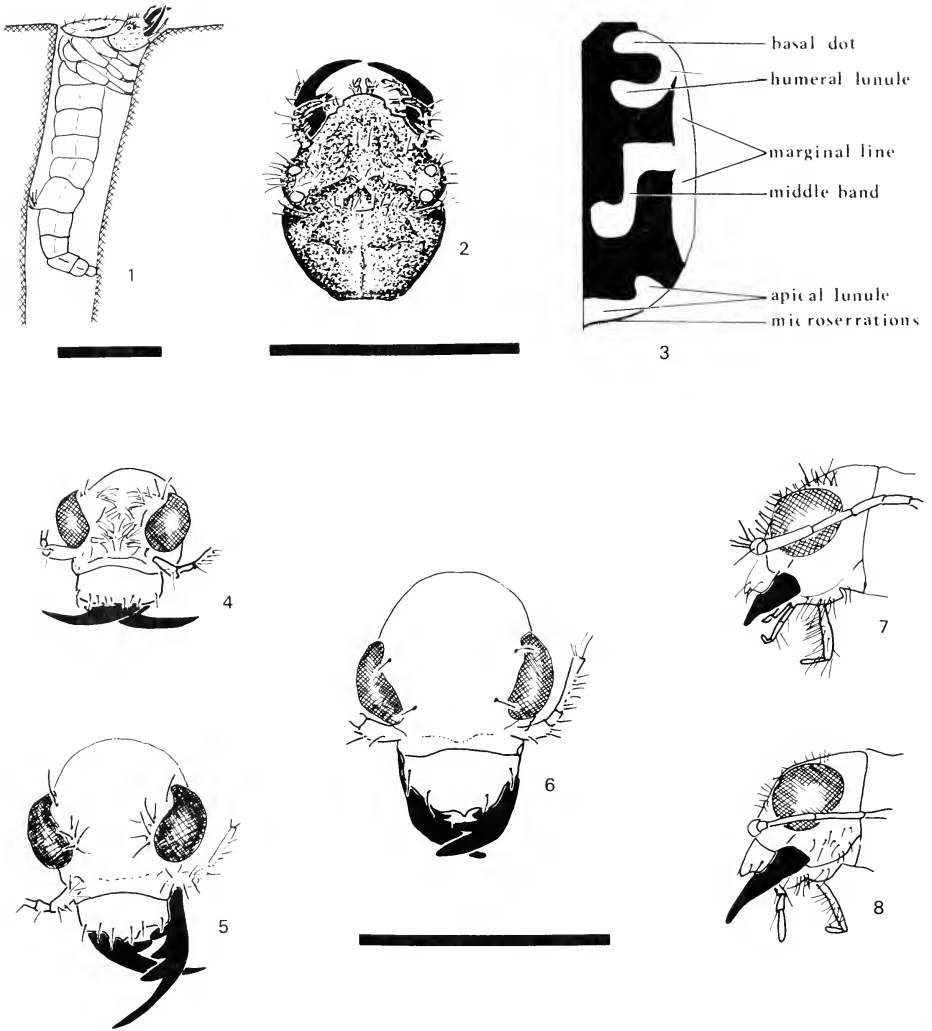
ACKNOWLEDGEMENTS

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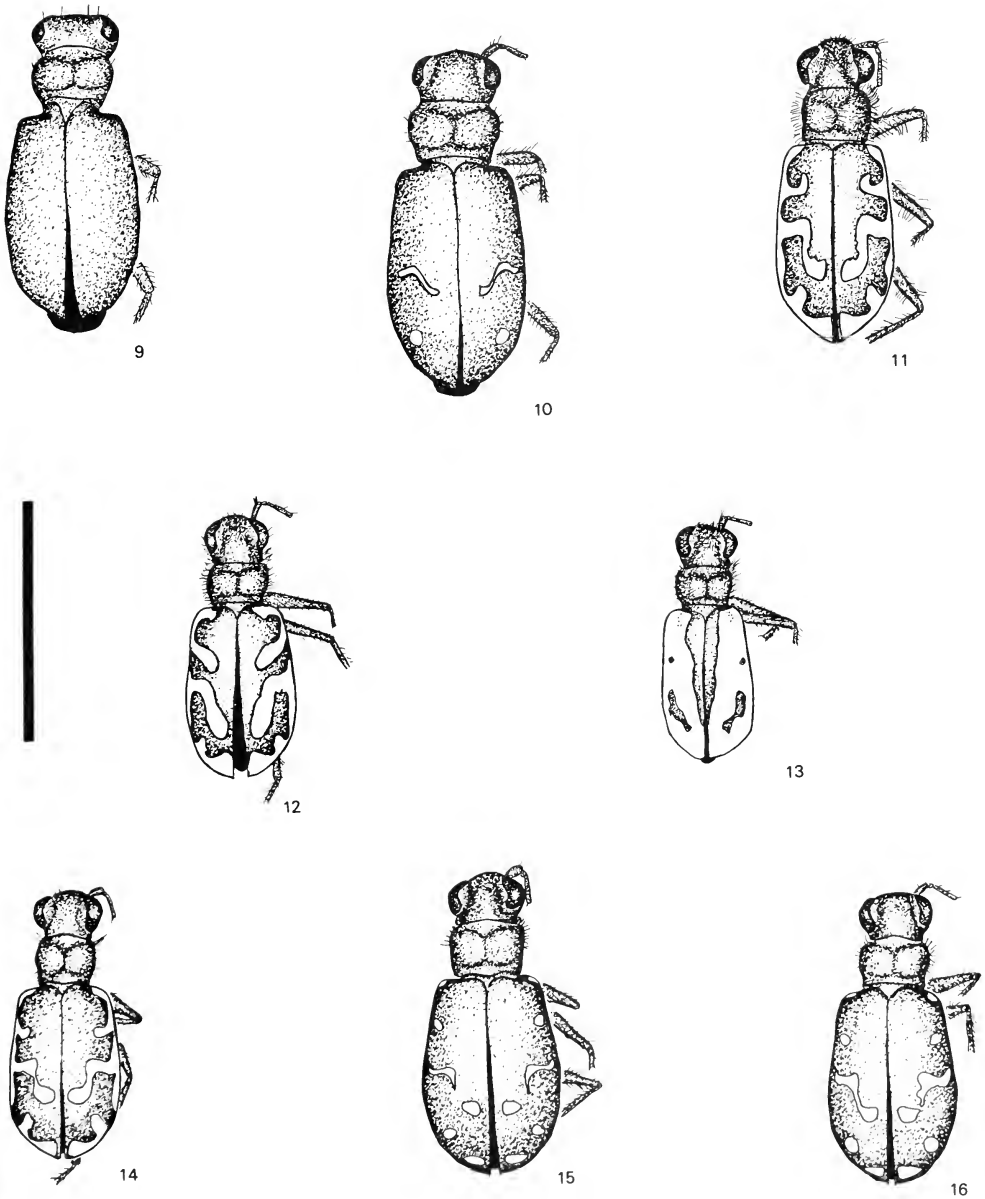
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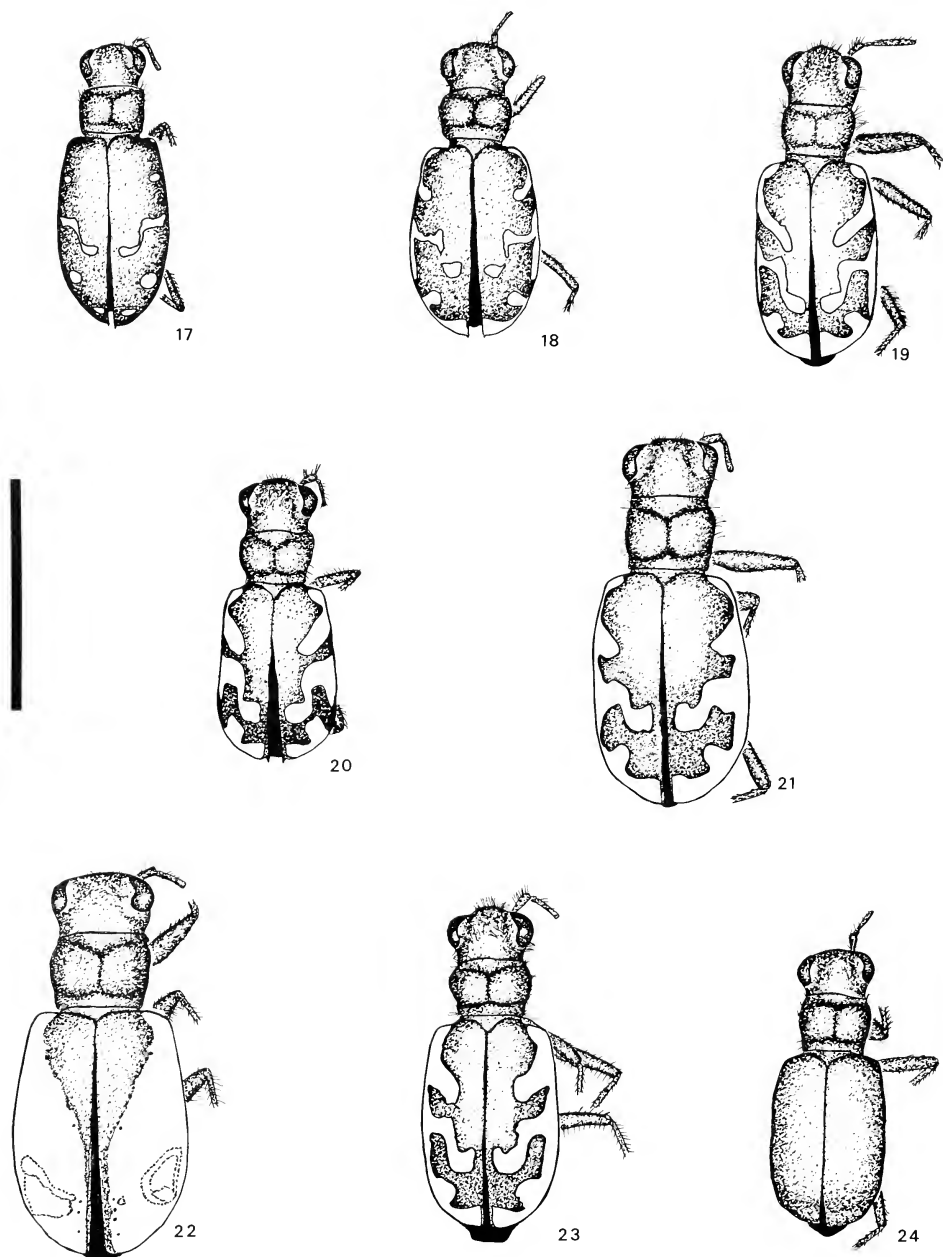
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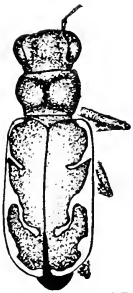
Figures 1-8. Drawings of larva and character states on adults. Scale line = 5 mm. Fig. 1. Habitus of generalized *Cicindela* larva. Fig. 2 Larval head and prothorax of *C. oregona oregona*, Osoyoos, B.C. Fig. 3. Generalized maculation pattern with nomenclature used. Fig. 4. Hairy head; *C. limbata nympha*. Fig. 5. Head with culstered hairs on inner margin of each eye; *C. scutellaris*. Fig. 6. Glabrous head; *C. nebraskana*. Fig. 7. Glabrous genae; *C. fulgida*. Fig. 8. Hairy genae; *C. duodecimguttata*.



Figures 9-16. Adult tiger beetles, line drawings, color refers to normal range, locality refers to where the specimen was collected. Scale line = 10 mm. Fig. 9. *C. nebraskana*; black; Empress, Alta. Fig. 10. *C. longilabris*; black to green; Fedora, Alta. Fig. 11. *C. hirticollis*; brown to olive; Gull Lake, Alta. Fig. 12. *C. limbata hyperborea*; brown; Fort MacKay, Alta. Fig. 13. *C. limbata nympha*; brown to greenish; Crimson Lake, Alta. Fig. 14. *C. repanda*; brown; Edmonton, Alta. Fig. 15. *C. oregona oregona*; brown, green, blue; Summerland, B.C. Fig. 16. *C. oregona guttifera*; brown; Kootenay Plains, Alta.



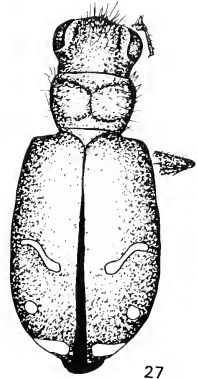
Figures 17-24. Adult tiger beetles, line drawings, color refers to normal range, locality refers to where the specimen was collected. Scale line = 10 mm. Fig. 17. *C. oregona* X *C. duodecimguttata*; brown; Carbondale River, Alta. Fig. 18. *C. duodecimguttata* brown; Stauffer, Alta. Fig. 19. *C. tranquebarica*; grey to brown; Calgary, Alta. Fig. 20. *C. fulgida*; coppery to metallic green; Lost River (near Onefour), Alta. Fig. 21. *C. formosa formosa*; red violet; Empress (11 km south), Alta. Fig. 22. *C. formosa gibsoni*; red to violet; Maple Creek (16 km north), Sask. Fig. 23. *C. lengi versuta*; rust, rarely green, blue, or black; Chappice Lake, Alta. Fig. 24. *C. scutellaris scutellaris*; red-green; Empress (11 km south), Alta.



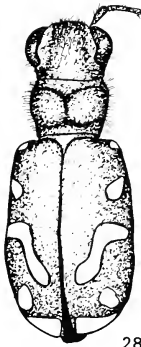
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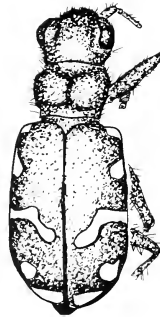
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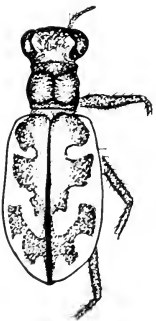
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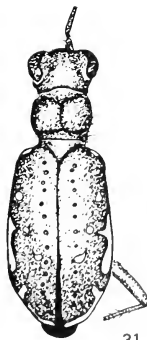
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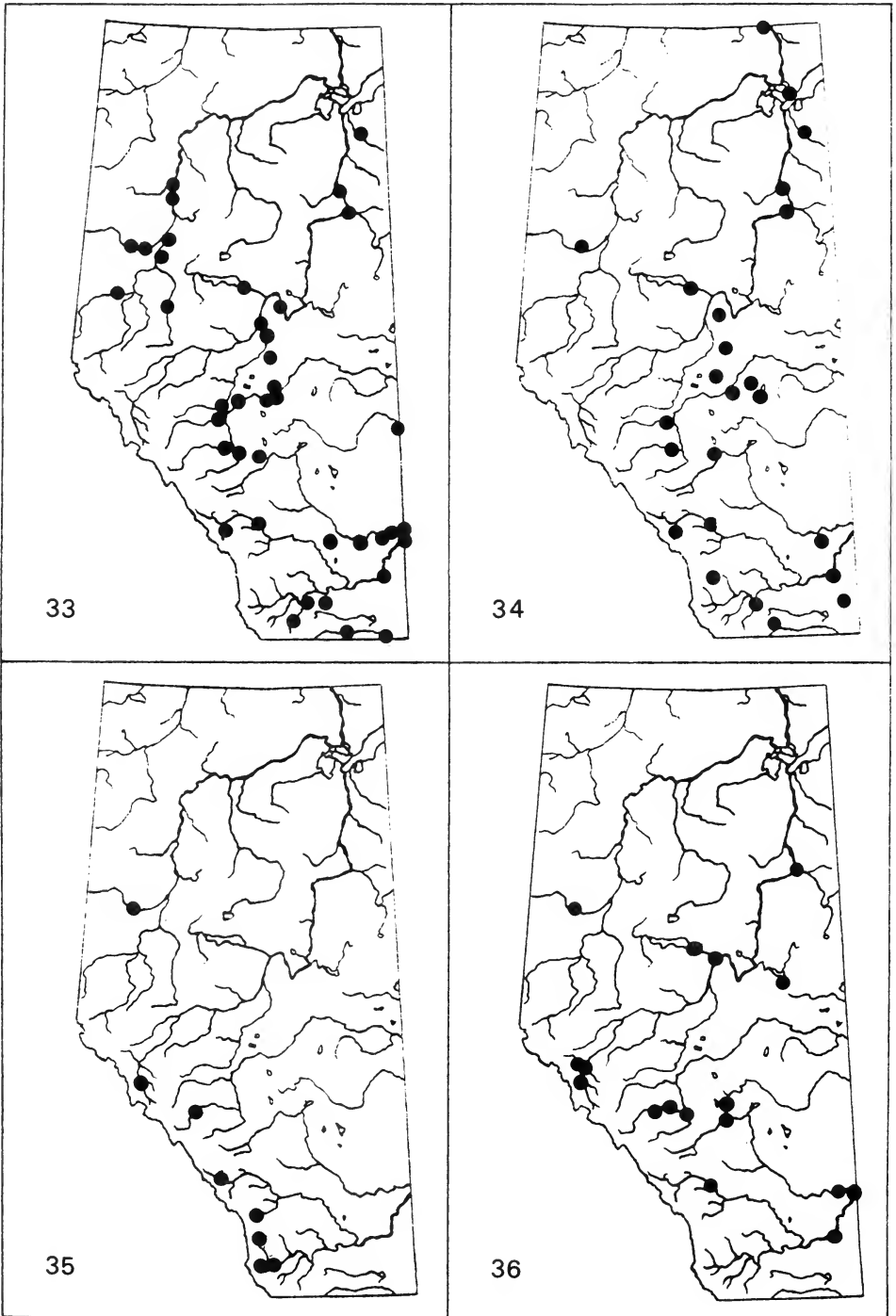


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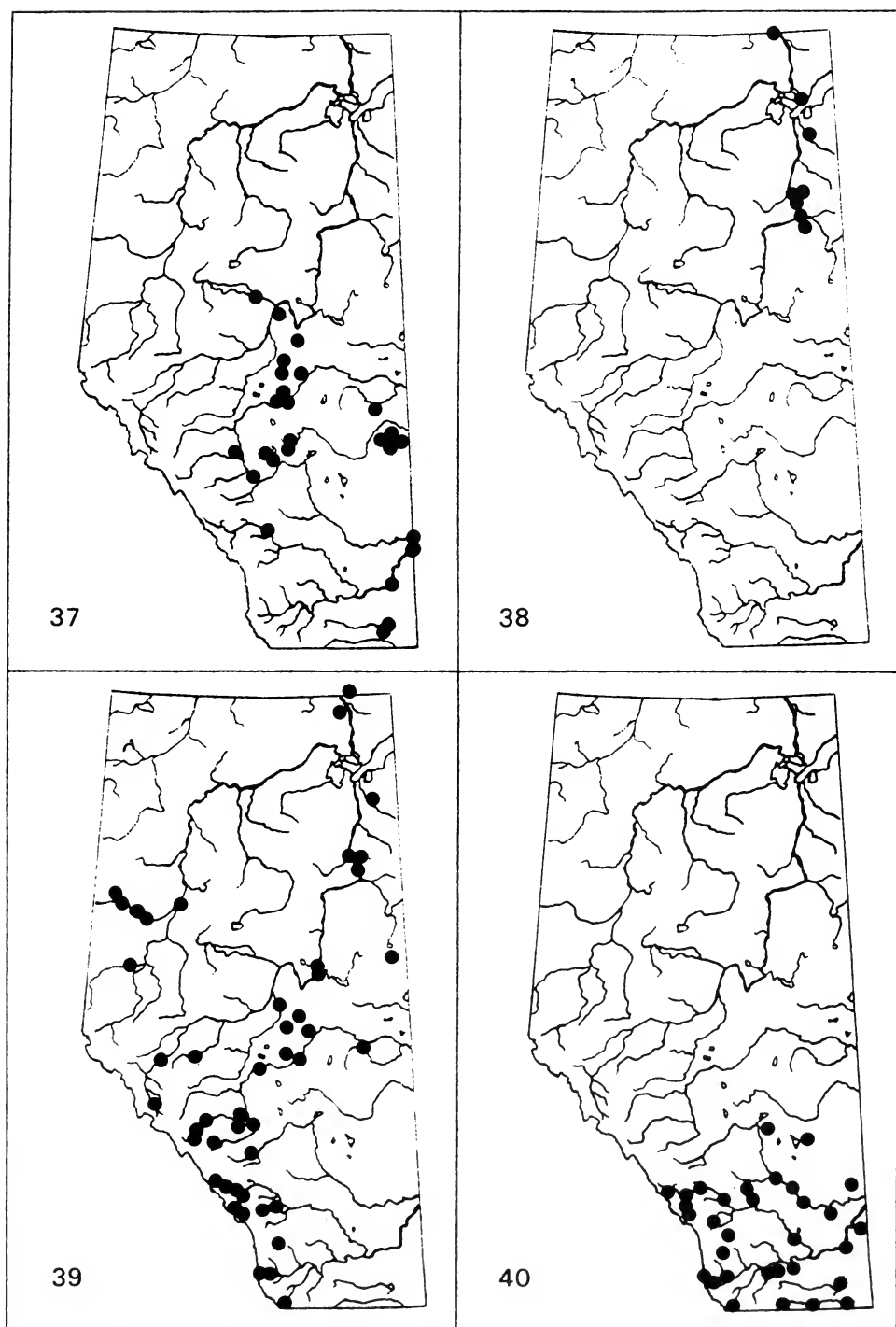


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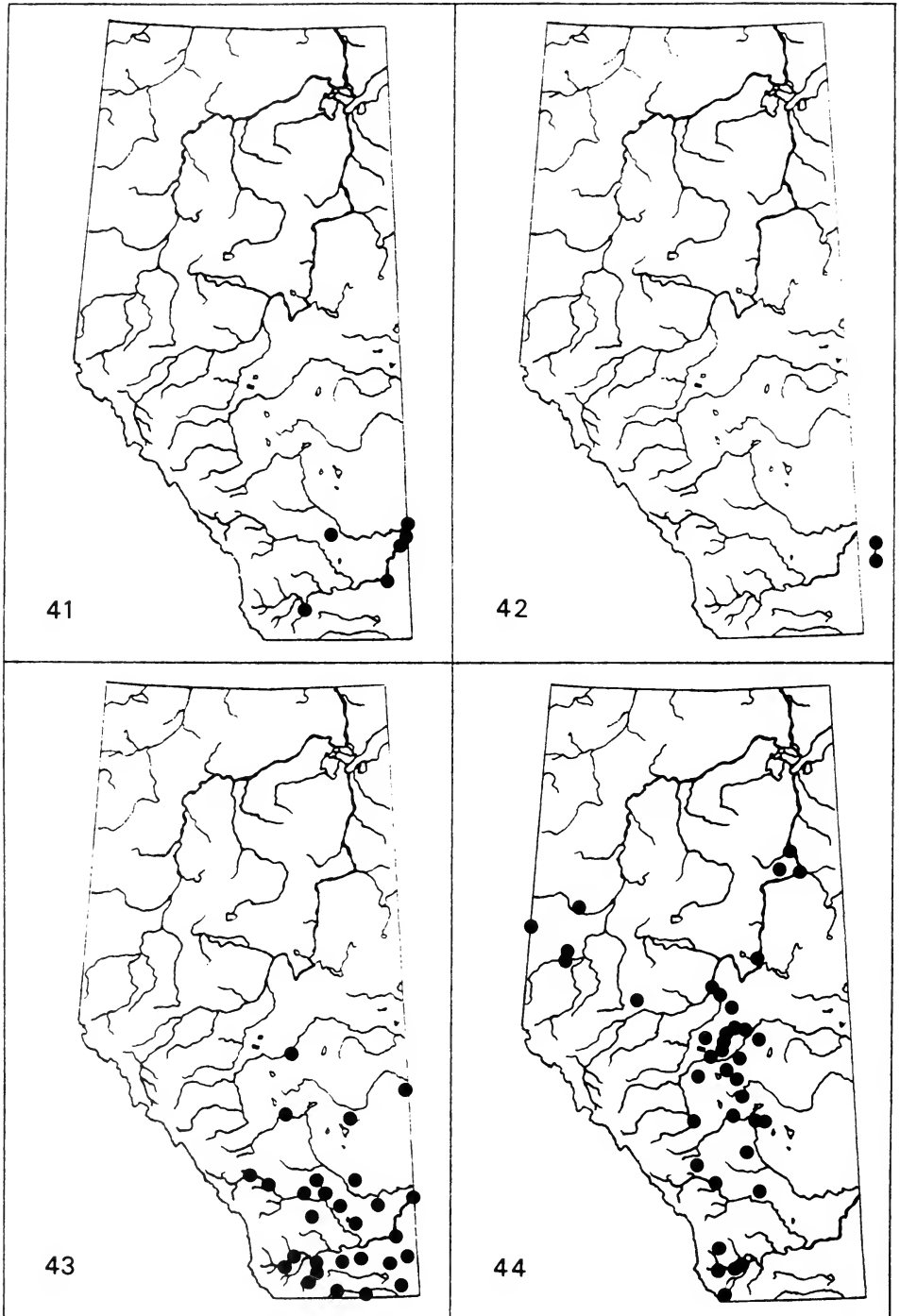
Figures 25-32. Adult tiger beetles, line drawings, color refers to normal range, locality refers to where the specimen was collected. Scale line = 10 mm. Fig. 25. *C. terricola cinctipennis*; green to olive; Calgary, Alta. Fig. 26. *C. terricola imperfecta*; green to olive; Kootenay Plains, Alta. Fig. 27. *C. purpurea*; green or black; Lost River (near Onefour), Alta. Fig. 28. *C. decemnotata*; green; Lethbridge, Alta. Fig. 29. *C. splendida limbalis*; red to green; Crimson Lake, Alta. Fig. 30. *C. nevadica knausi*; copper to brown; Jenner Ferry, Alta. Fig. 31. *C. punctulata*; grey brown; Empress (11 km south), Alta. Fig. 32. *C. lepida*; pale with brown; Empress (11 km south), Alta.



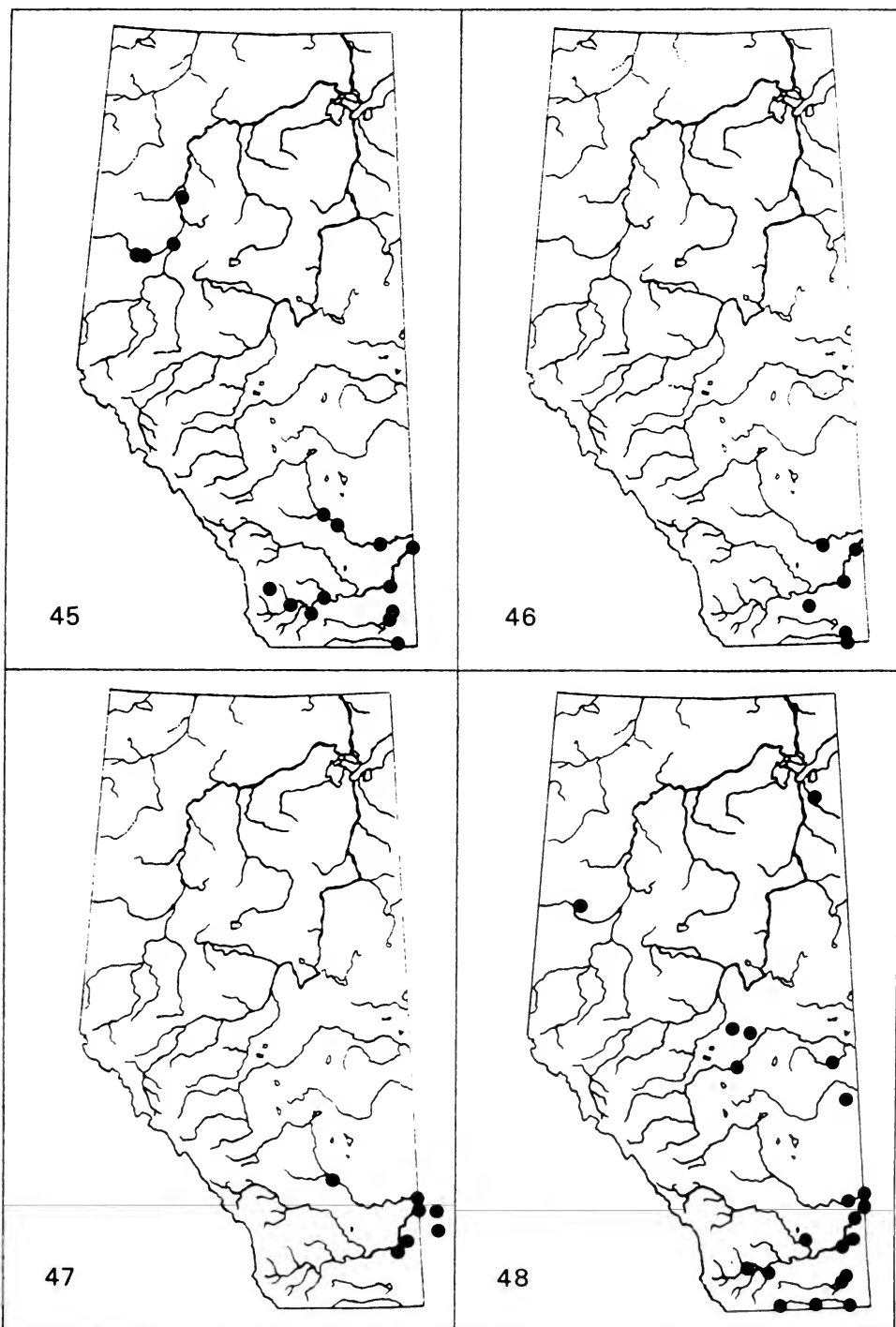
Figures 33-36. Distribution maps. Fig. 33. *C. repanda*. Fig. 34. *C. duodecimguttata*. Fig. 35. *C. oregona*. Fig. 36. *C. hirticollis*.



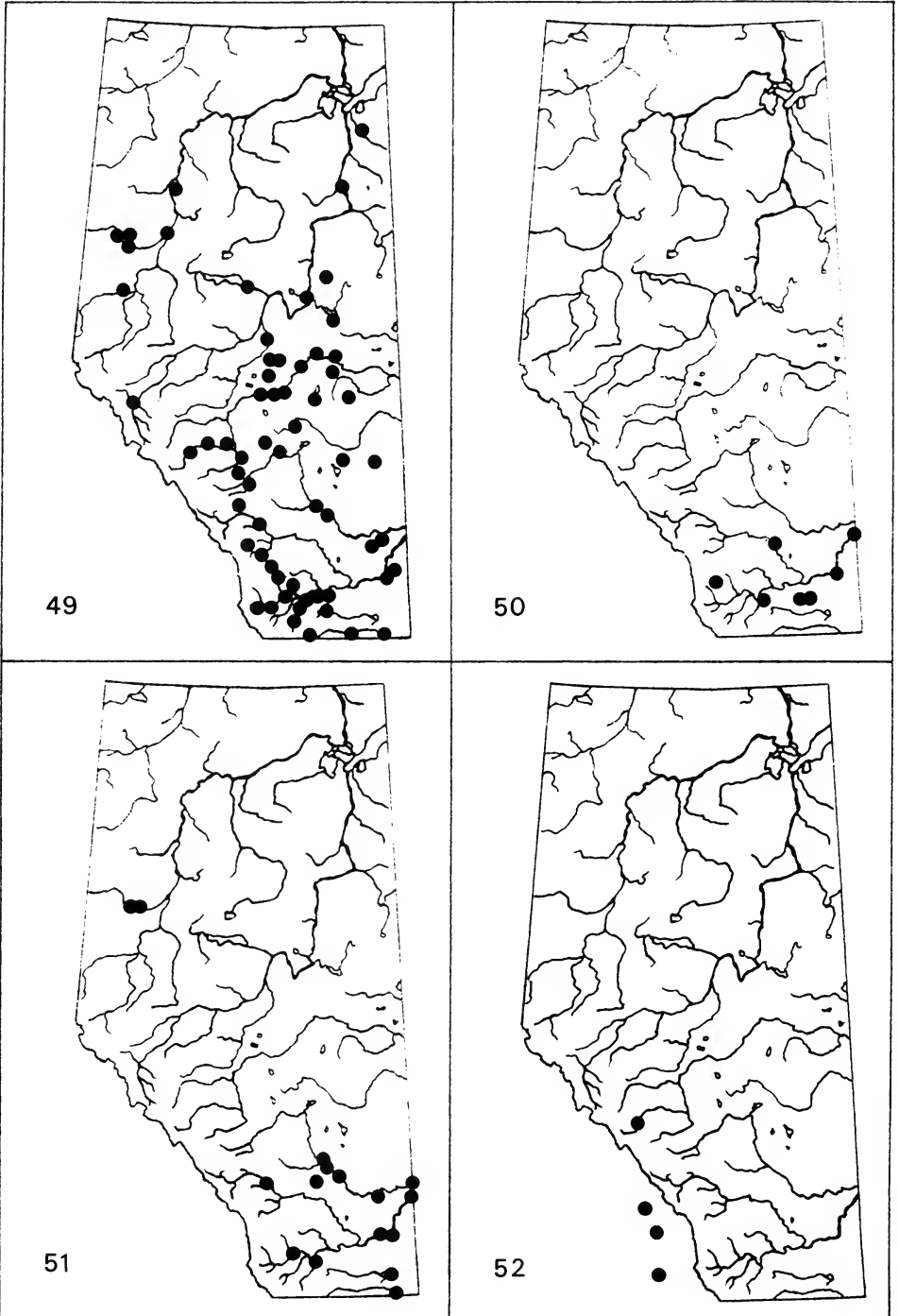
Figures 37-40. Distribution maps. Fig. 37. *C. limbata nympha*. Fig. 38. *C. limbata hyperborea*. Fig. 39. *C. longilabris*. Fig. 40. *C. nebraskana*.



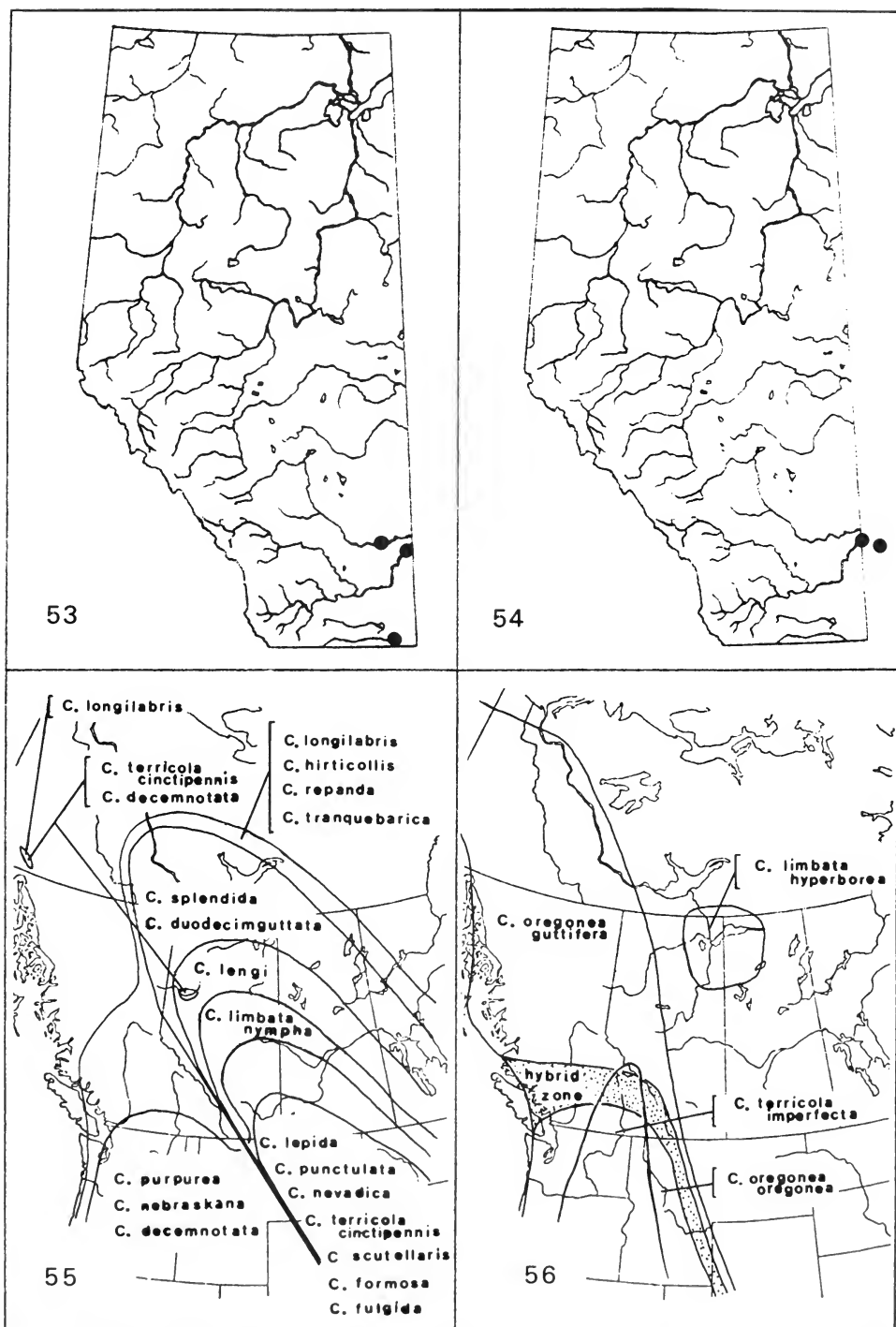
Figures 41-44. Distribution maps. Fig. 41. *C. formosa formosa*. Fig. 42. *C. formosa gibsoni*. Fig. 43. *C. purpurea*. Fig. 44. *C. splendida limbalis*.



Figures 45-48. Distribution maps. Fig. 45. *C. decemnotata*. Fig. 46. *C. fulgida*. Fig. 47. *C. scutellaris scutellaris*. Fig. 48. *C. lengi versuta*.



Figures 49-52. Distribution maps. Fig. 49. *C. tranquebarica*. Fig. 50. *C. punctulata*. Fig. 51. *C. terricola cinctipennis*. Fig. 52. *C. terricola imperfecta*.



Figures 53-56. Distribution maps. Fig. 53. *C. nevadica knausi*. Fig. 54. *C. lepida*. Fig. 55. Composite distribution map of tiger beetle species believed to have dispersed into Alberta from the southern Great Plains. Fig. 56. Composite distribution map of tiger beetle species believed to have dispersed into Alberta from the north, west and east.

CHARACTERISTICS AND EVOLUTION OF ELYTRAL SCULPTURE IN THE TRIBE GALERITINI (COLEOPTERA: CARABIDAE)¹

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ABSTRACT

A reconstructed phylogeny, based primarily on structural features other than details of the elytral cuticle, provides the basis for inferring evolution of macrosculpture and microsculpture of the elytra of galeritine adults. Macrosculpture consists of a system of alternating linear depressions (interneurs) and elevations (intervals). A transformation series extends in the subtribe *Galeritina* from primary intervals that are broad and slightly convex (or flat) to costate to carinate, with or without development of secondary intervals. In the monobasic more plesiotypic subtribe *Planetina*, the elytra have developed carinate primary and secondary intervals independently of these features in the more highly evolved groups of subtribe *Galeritina*. Within some taxa of *Galeritina*, the secondary intervals (carinulae) have been reduced or lost. The microsculpture system of microlines and included sculpticells has undergone a complex series of changes in the *Planetina* and *Galeritina*. Independently, in both subtribes, the plesiotypic microlines have been lost, and sculpticells are represented by nodules, which are only parts of the original sculpticells. In the genus *Eunostus* Castelnau (subtribe *Galeritina*), the plesiotypic microlines are evident, and sculpticells are transverse and flat, but a few exhibit small nodules. Convergence is postulated between *Planetina* and *Galeritina* with independent development of the same type of macrosculpture and microsculpture, and also within the *Galeritina*, with independent reduction in different lineages of the system of carinae and carinulae. The patterns of macrosculpture and microsculpture are correlated to the extent that adults with carinate intervals exhibit elongate sculpticells with transversely aligned nodules. This relationship may be the result of: 1) selective forces acting similarly on different genes to produce a functional complex; or 2) there may be a developmental constraint, such that ontogenetic development of carinae somehow channels or influences development of the derived form of microsculpture. If alternative 1 is correct, the derived, correlated forms of macrosculpture and microsculpture may be accepted as discrete character states for evaluation of phylogenetic relationships; if alternative 2 is correct, the derived pattern of macrosculpture and microsculpture must be regarded as a single character state. The biological significance of these transformation series is unknown, though the transverse form of sculpticells is generally correlated in other carabids with life in tightly packed leaf litter. The system of longitudinal carinae and sculpticells is reminiscent of a corrugated iron roof, and may be especially effective for shedding water and debris. Because this latter form of sculpture is exhibited by related species that have strikingly different

¹Based on the text of an address presented to the XVII International Congress of Entomology, Hamburg, Federal Republic of Germany, August, 1984

ecological requirements, the additional inference is made that sculpture is not responding to specific environmental factors, but rather to factors that are more general.

RÉSUMÉ

Une reconstruction de la phylogénie des Galeritins, établie principalement à partir de caractères structuraux autres que les détails de la cuticule élytrale, nous sert de base pour déduire les étapes évolutives de la macrosculpture et de la microsculpture des élytres chez les Galeritins adultes. La macrosculpture consiste en un ensemble de sillons (interneures) alternant avec des élévations linéaires (intervalles). Dans la sous-tribu des Galeritina, il existe une série de transformations des intervalles primaires qui passent de larges et légèrement convexes (ou aplatis) à costés ou carénés, avec ou sans apparition d'intervalles secondaires. Dans la sous-tribu monogénérique des Planetina, qui constitue un groupe plus plésiotypique, les élytres ont développé des carènes primaires et des intervalles secondaires indépendamment de ceux qu'on retrouve dans les groupes plus évolués de la sous-tribu des Galeritina. Chez certains taxons des Galeritina, il y a réduction ou perte des intervalles secondaires (carénules). La microsculpture, comprenant un ensemble de microlignes et de «sculpticellules», a subi une série complexe de changements chez les Planetina et les Galeritina. Indépendamment dans les deux sous-tribus, les microlignes plésiotypiques ont disparu et les «sculpticellules» n'existent plus qu'à l'état de nodules qui correspondent à une partie des «sculpticellules» originelles. Chez le genre Eunostus Castelnau (de la sous-tribu des Galeritina), les microlignes plésiotypiques sont évidentes et les «sculpticellules» sont transverses et aplaties, mais certaines «sculpticellules» montrent de petits nodules. Nous postulons qu'il y a eu convergence, d'une part entre les Planetina et les Galeritina lors du développement d'un type semblable de macrosculpture et de microsculpture, et d'autre part parmi les Galeritina où il y a eu réduction du système de carènes et de carénules de façon indépendante dans les différentes lignées. Les motifs de macrosculpture sont corrélés avec ceux de microsculpture dans la mesure où les adultes ayant des intervalles carénés possèdent des «sculpticellules» allongées avec des nodules alignés transversalement. Cette relation peut être le résultat soit de forces sélectives agissant similairement sur des gènes différents pour produire un ensemble fonctionnel, soit de contraintes de développement qui font que, d'une certaine façon, l'ontogénèse des carènes canalise ou influence le développement du type dérivé de microsculpture. Si la première alternative est correcte, nous pouvons accepter les types dérivés et corrélés de macrosculpture et de microsculpture comme étant des états de caractères distincts pour l'évaluation des relations phylogénétiques; par contre, si la seconde alternative est correcte, le motif dérivé de macrosculpture et de microsculpture doit être considéré comme un seul état de caractère. La signification biologique de ces séries de transformations est inconnue, bien que la présence de «sculpticellules» transverses est généralement corrélée, chez d'autres Carabiques, avec un mode de vie dans la litière compacte. Le système de carènes et de «sculpticellules» longitudinales fait penser à un toit de tôle ondulée et peut être particulièrement efficace pour se débarrasser de l'eau et des débris. Étant donné que ce dernier type de sculpture se rencontre chez des espèces apparentées qui possèdent des exigences écologiques fort différentes, nous déduisons par surcroît que la sculpture n'est pas assujettie à des facteurs environnementaux spécifiques, mais plutôt à des facteurs plus globaux.

INTRODUCTION

Most of what is known about galeritine carabids is summarized in various comparatively recent taxonomic treatments: Basilewsky (1963), Afrotropical species, Reichardt (1965 and 1967), the Asian species of *Galerita*, and the species of Galeritini in the New World, respectively; Lindroth (1969: 1091), and Ball and Nimmo (1983), species of the predominantly Nearctic subgenus *Progaleritina*.

The tribe Galeritini is pan-tropical, with northern extensions into the Nearctic (northward to southern Ontario and Québec) and eastern Palaearctic (northward to the Japanese Archipelago and southern Korea) Regions. Habitats occupied range from waterside stations and the rain forest floor in the tropics to dry open forests and savannas. Most species live at low altitudes, but in the American tropics, a number of species are known from montane forest.

Adults and larvae of all species are probably predators on other arthropods, though this has been shown for only a few species. It seems reasonable to make the extrapolation, because of general similarity in body form and details of the mouthparts among all taxa. Females of *Galerita* (*Progaleritina*) *bicolor* Drury lay their eggs in mud balls which are then attached to the undersides of leaves. This behavior is correlated with a peculiarly modified ovipositor,

which is characteristic of the more highly evolved galeritines. By extrapolation, it seems likely that all such taxa have similar habits, and that those with more plesiotypic ovipositors have more plesiotypic habits, and probably lay eggs in cavities in the soil, as do most female carabids. Adults of many of the macropterous species are found at lights, at night, showing that they are nocturnal and that they fly. Little else is known about ecological aspects of galeritines.

Although knowledge of galeritines is markedly restricted, I was able to make a reconstructed phylogeny, using previously studied features of adults, and adding analyses of structure of the mandibles and ovipositor (Ball, in press). Macrosculpture of the elytra was used to reconstruct the phylogeny of *Galerita* (*sensu lato*), but microsculpture was not studied in detail. Subsequently, I realized that elytral sculpture exhibited some interesting complexity, so I asked if patterns of sculptural variation might be correlated with the reconstructed phylogeny that I had made. Results are presented below.

MATERIAL AND METHODS

Material

The adults studied were those on hand that had been collected by me, were in the Strickland Museum of my Department, or were borrowed from other institutions for the phylogenetic study of the Galeritini. In aggregate, they represented a reasonably diverse cross-section of the tribe, but not all species. Sculpture of the elytra was examined superficially using representatives of the following taxa: *Planetes bimaculatus* MacLeay, *P. ruficollis* Nietner, *P. pendleburyi* Andrewes, and *Planetes* species?; *Eunostus herrarensis* Alluaud, *E. vuilloti* Alluaud, *Eunostus* new species; *Ancystroglossus ovalipennis* Reichardt, *A. dimidiaticornis* Chaudoir, and *Ancystroglossus* new species; *Trichognathus marginipennis* Latreille; and all seven species of *Galerita*, subgenus *Progaleritina*. From subgenus *Galerita*, I examined specimens of *G. perrieri* Fairmaire, *G. sulcipennis* Reichardt, various members of eight New World sub-groups: *americana*, *carbonaria*, *costulata*, *gracilis*, *jelskii*, *occidentalis*, *striata*, and *unicolor*; and four species of the *G. africana* group.

Detailed examination of microsculpture was made for specimens of *Planetes bimaculatus*, *Eunostus herrarensis*, *Ancystroglossus ovalipennis*, *Trichognathus marginipennis*, *Galerita mexicana* Chaudoir, *G. sulcipennis*, *G. perrieri*, *G. ruficollis* Dejean, *G. boucardi* Chaudoir, *G. balli* Reichardt, *G. attelaboides* Fabricius, and *G. procera* Gerstaecker.

Methods

Preparation and study of specimens.—Elytra of specimens chosen for superficial study were cleaned initially with ammonia applied with a moistened bit of tissue paper held in forceps. These specimens were examined with a Wild M5 Stereo-binocular microscope, at 50X magnification. On the basis of such examination, major types of sculpture were identified and specimens representing each type were selected for detailed examination.

For such study, except for the specimen of *G. perrieri*, the left elytron was removed, cleaned in water using a sonicator, attached to a standard mount, and coated with gold using a sputter coater. Specimens were examined and photographed, using a Cambridge S-250 "Stereoscan" Scanning Electron Microscope. The specimen of the rare Madagascan *G. perrieri*, was examined with its elytra attached to the body, uncoated, at relatively low magnifications of the SEM.

Analytical procedures.— These concerned identification of ancestral features of sculpture for each of the branching points of a tree that represented the reconstructed phylogeny of the

suprageneric groups of Galeritini. The general method used was hypothesis of transformation series (Figs. 2 and 5) polarized with the premises that flat (or slightly convex) elytral intervals are plesiotypic features of macrosculpture, and an isodiametric pattern with flat, non-imbricate sculpticells is the plesiotypic condition of the microsculpture. The latter premise is based on conclusions reached by Hinton (1970: 41-42), and Lindroth (1974).

The sequence of stages proposed in evolution of macrosculpture and microsculpture follows from the reconstructed phylogeny of Galeritini (Fig. 1, from Ball [in press]). For each pair of sister groups, the sculpture pattern most like the proposed ancestral pattern was judged the more plesiotypic, and accepted as the ancestral pattern for that pair of sister taxa. Transformation series for macrosculpture and microsculpture were established separately. The separate analyses are presented together on diagrams representing the reconstructed phylogeny of Galeritini (Figs. 7 and 8).

SCULPTURE OF THE ELYTRA

For purposes of this presentation, the term "macrosculpture" refers to the alternating system of longitudinal convexities (intervals) and concavities (interneurs) on the surface of a typical elytron. Intervals mark the areas which are the courses of veins of the fore wing (Jeannel, 1941: 30-31). "Microsculpture" refers to the network of fine lines and microscopic sculpticells (Allen and Ball, 1980: 486) that cover the surface. This network, in its most plesiotypic form, reflects the form of the cellular network of the underlying epidermis (Hinton, 1970: 41-42). Types of macrosculpture are designated by Roman numerals and capital letters; microsculpture types are designated by Arabic numerals and capital letters.

Macrosculpture

Within the tribe Galeritini, intervals range in form from broad and flat (Fig. 2, Type I) to broad and convex (costate, Fig. 2, Type III), to narrow and convex (carinate, Fig. 2, types II-IV). An elytron exhibits a simple arrangement, with all intervals being equal in width and convexity, or a complex arrangement, with a pair of secondary intervals (carinulae) intercalated between adjacent broader, primary intervals (carinae, Fig. 2, Subtype IVA, and Fig. 3). The number of carinae is either nine (Fig. 2, Subtype IIa, and Type IV), or five (Subtype IIB).

Microsculpture

At magnifications of about 50X, the cuticle of most arthropods exhibits a mesh of fine lines, like the lines of a fish net (Lindroth, 1974: 252, and Allen and Ball, 1980: 485-486). Meshes are characterized as isodiametric, transverse, or longitudinal, depending upon their relative lengths and widths. "Sculpticells" (Allen and Ball, 1980: 486) between microlines range in form from flat to slightly or markedly convex, to carinate (Ball, 1975: Fig. 114).

Galeritines exhibit a variety of forms of microsculpture. At the base of an elytron, sculpticells are flat, slightly imbricate (Harris, 1979: 19 and 30, Fig. 40). and nearly isodiametric (Fig. 6), or transverse (Fig. 4). Most of the elytral surface is:

- a. covered with a network of transverse meshes (some sculpticells with posterior nodules, Fig. 5, Type 1); or
- b. with nodule-like swellings, either not arranged in a pattern (Subtypes 2A and B), or aligned transversely (Types 3 and 4).

RECONSTRUCTED PHYLOGENY OF TRIBE GALERITINI

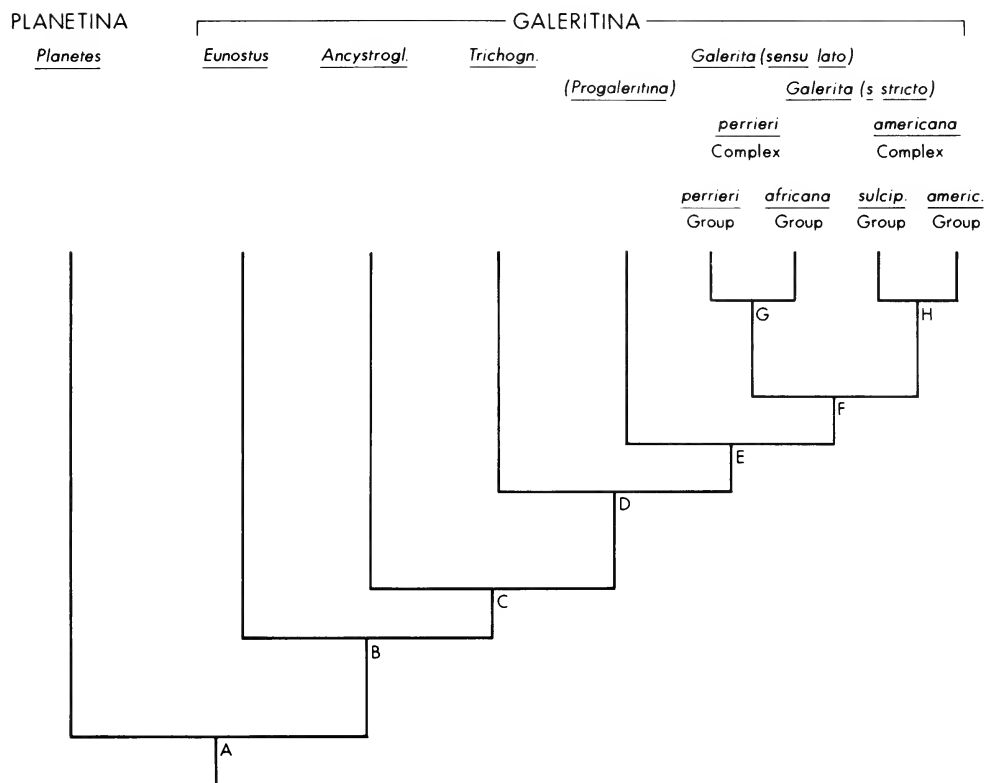


Fig. 1. Reconstructed phylogeny of Tribe Galeritini. Taxa are: Subtribe Planetina - *Planetes* MacLeay; Subtribe Galeritina - *Eunostus* Castelnau; *Ancystroglossus* Chaudoir; *Trichognathus* Latreille; *Galerita (sensu lato)* - subgenus *Progaleritina* Jeannel, and subgenus *Galerita* Fabricius, including the *G. perrieri* complex (with *G. perrieri* and *G. africana* groups), and the *G. americana* complex (with *G. sulcipennis* and *G. americana* groups).

The general term for sculpture of Types 2, 3, and 4 is nodulate (Harris, 1979: 15). As detailed below, each nodule is hypothesized as representing only part of an original sculpticell.

PHYLOGENETIC RELATIONSHIPS OF THE GALERITINI

A reconstructed phylogeny of the Galeritini (Fig. 1), based on features of adults (Ball, in press), provides a framework for an evolutionary analysis of sculpture patterns. Each node is designated by a capital letter (A-H), in alphabetical sequence, depending upon recency of common ancestry, except for the terminal two nodes. Aspects of elytral sculpture were used as a major feature to reconstruct the phylogeny of the supraspecific taxa of the genus *Galerita*, but

SUBTRIBE GALERITINA : TRANSFORMATION SERIES
IN MACROSCULPTURE OF ELYTRA

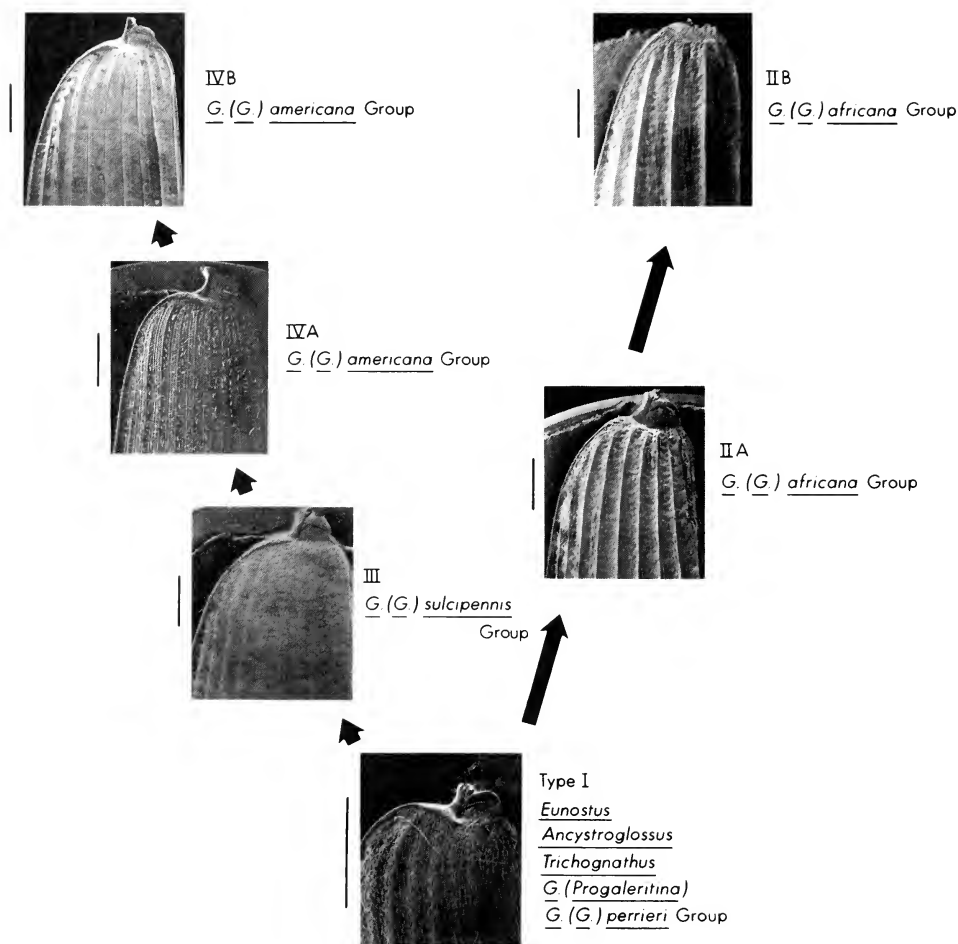


Fig. 2. Subtribe Galeritina: transformation series in macrosculpture of elytra. Types IIA-IVB represent approximately the basal one third, and Type I, the basal one quarter, of the left elytron. Species represented by illustrations are the following: Type I - *Eunostus herrarensis* Alluaud, *Ancystroglossus ovalipennis* Reichardt, *Trichognathus marginipennis* Latreille, *G. (Progaleritina) mexicana* Chaudoir, and *G. (Galerita) perrieri* Fairmaire; Subtype IIA - *G. (Galerita) attelaboides* Fabricius; Subtype IIB - *G. (Galerita) procera* Gerstaecker; Type III - *G. (Galerita) sulcipennis* Reichardt; Subtype IVA - *G. (Galerita) ruficollis* Dejean; and Subtype IVB - *G. (Galerita) balli* Reichardt. Scale bars represent 1.0 mm.

SUBTRIBE PLANETINA : Planetes
MACROSCULPTURE - LEFT ELYTRON

BASAL PORTION

DISC

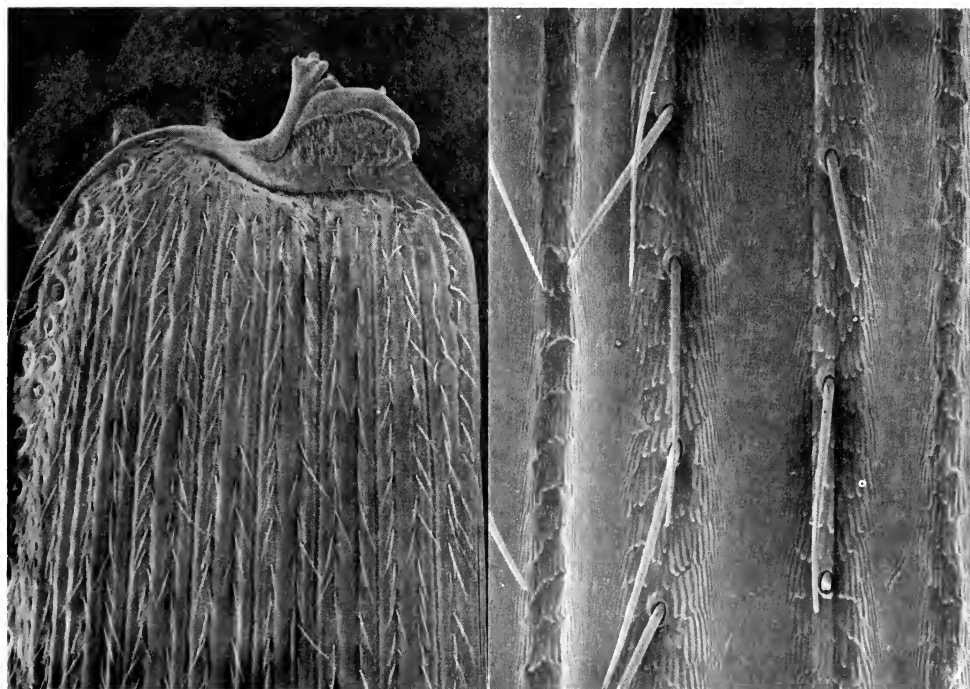


Fig. 3. Subtribe Planetina: macrosculpture of the left elytron of *Planetes bimaculatus* MacLeay. Scale bars represent 250 μm .

not to reconstruct the phylogeny of the other genera.

Overall, the system reflects important changes in structure of the mouthparts and ovipositor. There is also a striking increase in body size associated with node D, probably reflecting a change in habits from that of hunting concealed in the leaf litter to running on the surface of the forest floor, or in more open areas.

PATTERNS OF ELYTRAL SCULPTURE OF THE GALERITINI

Although the subtribe Planetina exhibits more plesiotypic features than does the Galeritina, outgroup comparison shows that planetine adults have highly derived sculpture. Thus, the subtribe Galeritina, with its greater range of sculpture types, is the focal group for elucidation

of evolution of these systems, and the following analyses begin with consideration of this subtribe.

Macrosculpture

Subtribe Galeritina.— Figure 2 illustrates the hypothesized trends in elytral macrosculpture. The figures also illustrate the reduced basal ridge that is characteristic of the adults of *Galeritina*. Four general types of macrosculpture are recognized, based on structural and phylogenetic considerations.

Type I includes elytra with broad intervals that are either flat or slightly convex. I did not formally distinguish between the slight difference involved. Type I is characteristic of three genera, and of one subgenus and one species group of *Galerita* (*sensu lato*).

Type II macrosculpture is characteristic of the *G. africana* group (*Galeritiola* Jeannel, of previous authors). It differs from Type I by having wider and deeper interneurs, and consequently narrower intervals, the latter being carinate. Two subtypes of macrosculpture are recognized: IIA, with nine carinae; IIB, with five carinae.

Type III macrosculpture is characteristic of the monobasic Middle American montane *G. sulcipennis* group. The elytral intervals are more elevated than in Type I, and are classified as costate. The figure, unfortunately, does not do justice to the difference between the two types of sculpture.

Type IV macrosculpture is characterized by carinae and readily seen carinulae (Subtype IVA), or if carinulae are not readily apparent, careful examination reveals vestiges of them (Subtype IVB). Subtype IVB looks very much like IIA, but the carinae of IVB are not as high, and the interneurs of IIA lack any indication of carinulae.

Subtribe Planetina.— Figure 3 illustrates macrosculpture for a specimen of *Planetes*. The pattern is Subtype IVA. Carinulae appear to be nearly as wide as the carinae, but in fact there is a substantial difference as the figure of a portion of the elytral disc, taken at higher magnification, indicates. At working magnifications (ca. 5X - 50X), however, the carinae and carinulae appear about equal, so that the elytra seem to have a densely packed system of carinae, and thus seem quite different from the Subtype IVA elytra of *Galerita*.

Microsculpture

Subtribe Galeritina.— Figure 4 illustrates two general types of microsculpture characteristic of galeritines: imbricate, which is confined to the basal area, principally basad of the basal ridge; and nodulate, which is more or less extensive on the disc. The sculpticells of the imbricate type are flat and broad, while the nodulate sculpticells are narrower and convex. Four types of microsculpture are recognized on the elytral disc in the *Galeritina*, and their proposed evolutionary trends are illustrated in Figure 5. Type I, which is characteristic of *Eunostus* the sister group of the other three galeritine genera, exhibits markedly transverse, flat sculpticells across most of the surface. Laterally, however, some sculpticells have small medio-apical nodules.

Types 2-4 are characterized by widespread nodulate microsculpture, without microlines. Type 2 exhibits a non-patterned arrangement of nodules, with Subtype 2A having fewer nodules than Subtype 2B. The former is characteristic of *Ancystroglossus*, the latter of *Trichognathus* and subgenus *Progaleritina*.

In Type 3 microsculpture, which is confined to the *G. perrieri* species complex, the nodules are in transverse rows: in 3A, exhibited by adults of the *G. perrieri* group, the nodules are short

MICROSCULPTURE AT BASE OF LEFT ELYTRON



Trichognathus marginipennis

Fig. 4. Macrosculpture at base of left elytron of *Trichognathus marginipennis* Latreille. Scale bar represents 150 μ m.

SUBTRIBE GALERITINA : TRANSFORMATION SERIES
IN MICROSCULPTURE OF ELYTRA

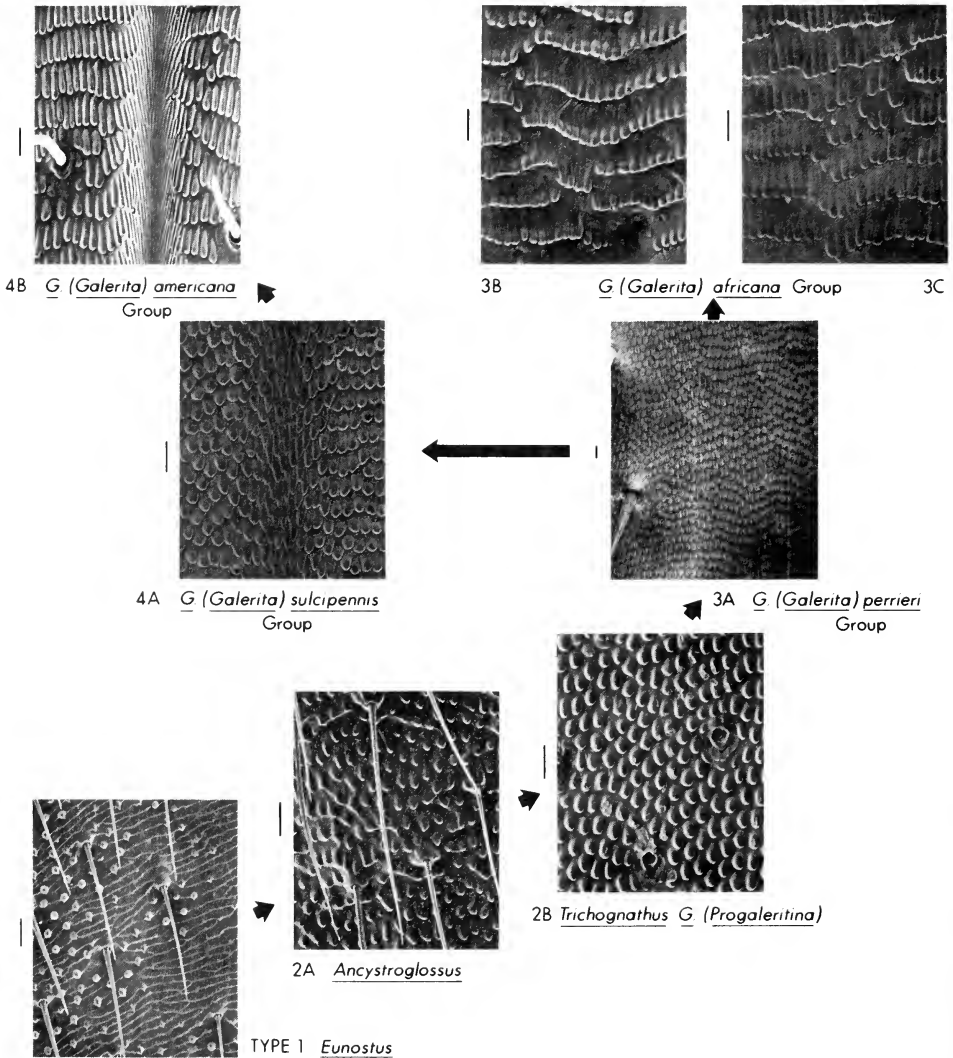


Fig. 5. Subtribe Galeritina: transformation series in microsculpture of elytra. Type I illustrates a portion of interneur 7 in the basal third of the left elytron. Subtypes 2A-4B illustrate portions of interneur 3 and/or 4, in the basal third of the left elytron. Species represented are: Type I - *Eunostus herrarensis* Alluaud; 2A, *Ancystroglossus ovalipennis* Reichardt; 2B, *Trichognathus marginipennis* Latreille, and *G. (Progaleritina) mexicana* Chaudoir; 3A, *G. (Galerita) perrieri* Fairmaire; 3B, *G. (Galerita) attelaboides* Fabricius; 3C, *G. (Galerita) procera* Gerstaecker; 4A, *G. (Galerita) sulcipennis* Reichardt; 4B, *G. (Galerita) ruficollis* Dejean. Scale bars represent 50 μ m.

SUBTRIBE PLANETINA : *Planetes* MICROSCULPTURE - LEFT ELYTRON

BASE

DISC

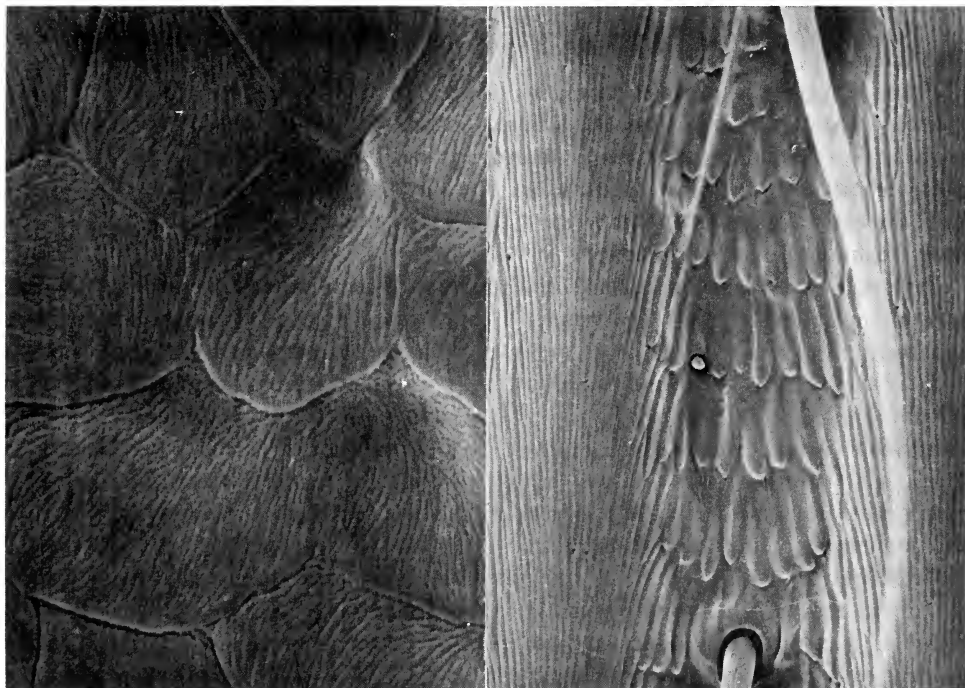


Fig. 6. Subtribe Planetina: microsculpture of the left elytron of *Planetes bimaculatus* MacLeay. The illustrations represent parts of the left elytron: the basal tenth, toward the sutural margin; and a portion of interneur 3 and adjacent carinulae. Scale bars represent 10 μ m.

and uniform across the elytral surface; for 3B and 3C, characteristic of the *G. africana* group, the nodules are longer than those of 3A, but *inter se* are relatively shorter (3B) or longer (3C), flattened basally, and in fairly well marked transverse rows, between carinae. On the tops of the carinae, the sculpticells are elongate and flat, and closely adpressed.

Type 4 microsculpture is exhibited by adults of the *G. americana* complex. Of the two Subtypes, 4A (*G. sulcipennis* group) is most like that of the *G. perrieri* group. The difference is seen in the elongate and flattened nodules on the top of the elytral costae. In Subtype 4B (exhibited by adults of the *G. americana* group), the nodules are longer and the transverse rows between adjacent carinae and carinulae are better defined. In those adults exhibiting Subtype IVB macrosculpture (*i.e.*, with carinae reduced), locations of atrophied carinulae are indicated

by the markedly elongate sculpticells that are a characteristic feature of the tops of carinae and carinulae.

Subtribe Planetina.— Figure 6 illustrates microsculpture characteristic of *Planetes* adults. The elytral base has imbricate, flat, and essentially isodiametric sculpticells. The disc exhibits long, keeled nodules arranged in transverse rows between adjacent carinae and carinulae. The sculpticells of the latter are very narrow and linear.

EVOLUTION OF ELYTRAL SCULPTURE OF THE GALERITINI

The Pattern

Figures 7 and 8 illustrate and summarize the hypothesis of evolution of sculpture. Figure 8 is a continuation of Fig. 7. For the labelled nodes except G, the hypothesized ancestral combination of sculptural features is illustrated, based on features of extant galeritines, macrosculpture above, microsculpture below. The ancestral states for node G are the same as for F. For each of the extant groups whose sculptural features differ from those of the ancestral stock, illustrations are also provided.

Features of the common ancestor.—These are inferred from the most plesiotypic sculptural features of extant adult galeritines. They are Type I macrosculpture, and imbricate-isodiametric microsculpture, the latter as seen on the elytral base of *Planetes* adults.

Macrosculpture.— The reconstructed phylogeny suggests that from Ancestor A to F or G in subtribe Galeritina, there were no significant changes in macrosculpture. From Ancestor G, with Type I macrosculpture, Type II developed, and further differentiated into two subtypes, in the *G. africana* group, with Subtype IIB losing four carinae. From Ancestor F, Type III sculpture emerged in Ancestor H, and from the latter, Type IV, which in turn differentiated into two subtypes, in the *G. americana* group.

To determine polarity of Type IV sculpture, I relied on correlation of characters, for this part of the transformation series is not ordained by the reconstructed phylogeny presented in Figure 1. Subtype IVB is associated with the derived features of brachyptery and life in montane environments, in the northern part of the Neotropical Region. Subtype IVA, on the other hand, is associated with the ancestral features of macroptery and life in lowland environments, over extensive areas of the tropics. Reichardt (1967: 158) postulated, and I agree, that the traces of carinulae are evidence of loss, associated with reduction of wings and loss of flight, rather than that the traces represent the precursors of fully developed carinulae.

Although there is no sign in Type III of developing carinulae, or widened interneurs to foreshadow development of Type IV sculpture, a costate condition (Type III) could be a reasonable step between nearly flat (Type I) and carinate (Type IV) conditions.

In the lineage that gave rise to the Planetina, macrosculpture Type IVA also arose. Although intermediate extant forms are unknown, it seems unlikely that the change from the postulated ancestral condition occurred without intermediate changes like those proposed for the Galeritina.

Microsculpture.— Although changes in macrosculpture came relatively late in the Galeritina lineage, the pattern for microsculpture suggests an early striking change, followed by less marked differentiation. I suggest that imbricate isodiametric sculpture of Ancestor A changed in Ancestor B to transverse sculpture, with some sculpticells exhibiting nodules. This was followed on the surface apicad of the basal ridge, by spread of the nodules over the disc, and disappearance of the plesiotypic lines that marked the sculpticells. The number of nodules increased, and took on an arrangement in rather irregular transverse rows (Ancestor F,

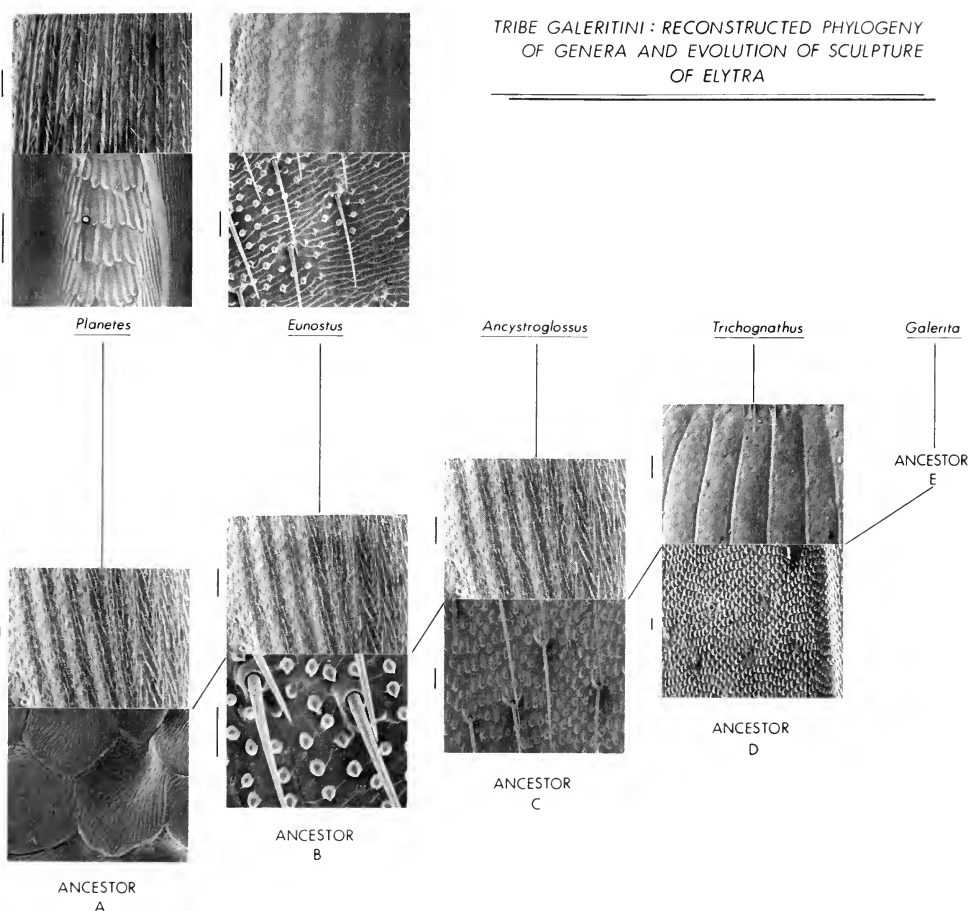


Fig. 7. Tribe Galeritini: reconstructed phylogeny of genera and evolution of sculpture of elytra. Sculpture of elytra of *Planetes*, *Eunostus*, and Ancestors A-D are each represented by a pair of figures, of which the lower is microsculpture, and the upper macrosculpture. The figure for Ancestor C also represents *Ancystroglossus*, and those for Ancestor D also represent *Trichognathus* and *Galerita*. The illustrations are of the left elytron, basal portion, as explained in captions for Fig. 2 (macrosculpture) and Fig. 5 (microsculpture). Specimens represented are: Ancestor A - microsculpture, *Planetes bimaculatus* MacLeay, and macrosculpture, *Ancystroglossus ovalipennis* Reichardt; *Planetes bimaculatus*; Ancestor B - microsculpture, *Eunostus herrarensis* Alluaud, and macrosculpture, *A. ovalipennis*; *Eunostus herrarensis*; Ancestor C, *A. ovalipennis*; Ancestor D, *Trichognathus marginipennis* Latreille. Scale bars represent at low magnification, 500 μ m; at high magnification, 50 μ m.

GENUS *Galerita*: RECONSTRUCTED PHYLOGENY
OF SUBGENERA, SPECIES COMPLEXES AND
GROUPS, AND EVOLUTION OF SCULPTURE
OF ELYTRA

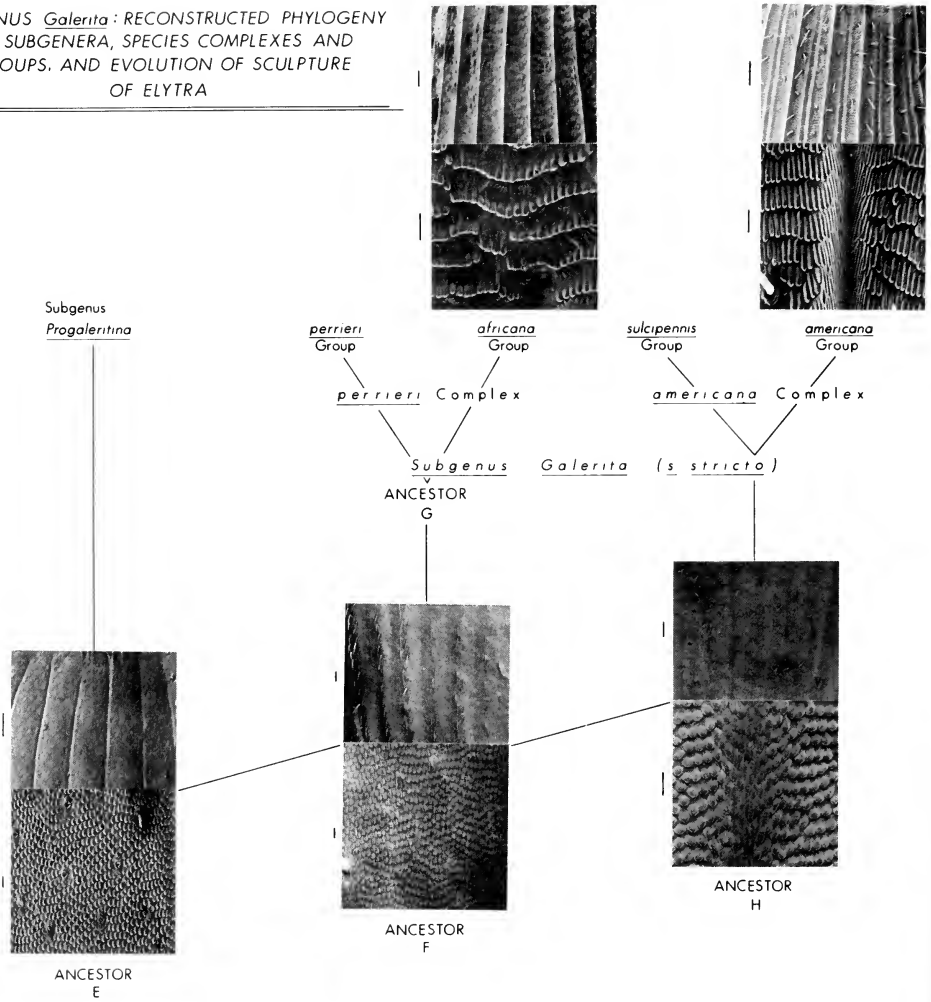


Fig. 8. Genus *Galerita*: reconstructed phylogeny of subgenera, species complexes and groups, and evolution of sculpture of the elytra. Sculpture of the elytra of Ancestor E, Ancestor F, the *G. africana* group, Ancestor H, and the *G. americana* group are each represented by a pair of figures, of which the lower is microsculpture and the upper macrosculpture. The figures for Ancestor E also represent subgenus *Progaleritina*; for Ancestor F, also Ancestor G and the *G. perrieri* group; for Ancestor H, also the *G. sulcipennis* group. The figures are of the left elytron, basal portion, as explained in the caption for Fig. 2 (macrosculpture) and Fig. 5 (microsculpture). Specimens represented are of these species: Ancestor E - *G. (Progaleritina) mexicana* Chaudoir; Ancestor F - *G. (Galerita) perrieri* Fairmaire; *G. africana* group - *G. (Galerita) attelaboides* Fabricius; Ancestor H - *G. (Galerita) sulcipennis* Reichardt; and *G. americana* group - *G. (Galerita) ruficollis* Dejean. Scale bars represent at low magnification, 500 μ m; at high magnification, 50 μ m, and at very high magnification, 5 μ m.

Subtype 3A). As a more complex macrosculpture evolved, the transverse rows of nodules were confined to the interneurs (Subtypes 3B, 3C, 4A, and 4B).

Subtype 3A microsculpture seems easily derived from Subtype 2B by development of a more orderly arrangement of nodules. Subtypes 3B and 3C are derived from 3A by a still more ordered arrangement of nodules, and possibly by fusion of pairs of nodules, in adjacent rows, to yield nodules that are fewer and longer. The transverse rows of nodules, confined to the interneurs (Subtypes 3B, 3C, 4A, and 4B), probably decreased in number by fusion of members of adjacent rows, and, consequently, the individual nodules became longer (Subtypes 3C and 4B). On the elytral base, transverse imbricate sculpture was retained. Transformation of 3A to 4A and the latter to 4B is virtually self-evident, paralleling the transformation of 3A to 3B, and to 3C.

It is important to note that the transverse sculpticells on the elytral disc of *Eunostus* adults are not imbricate. This change is interpreted as a loss, and a reversion to a state more plesiotypic than is exhibited by the sculpture of Ancestor A.

The planetine lineage adults evolved, on the elytral surface apicad of the basal ridge, nodulate microsculpture with long nodules, similar to that of Subtype 4B. As for the macrosculpture, intermediate steps are not known for evolution of the microsculpture, between the hypothetical ancestral condition and that of the extant species of *Planetes*. On the basal area of the elytra, the imbricate isodiametric sculpture was retained.

Microsculpture of the elytral base that is characteristic of *Planetes* seems the most plesiotypic pattern among extant Galeritini. The discal sculpture, on the other hand, is highly derived, with no known extant antecedents.

Convergence among taxa.— The same derived patterns of macrosculpture and microsculpture are represented in planetines and galeritines, and within distantly related members of the Galeritina. Adults of *Planetes* and of the *G. americana* group exhibit the complex type of elytral macrosculpture, with development of a system of alternating carinae and pairs of carinulae. Similarly, within the genus *Galerita*, a system of carinate intervals has evolved independently in different groups of the subgenus *Galerita*. Also, *Planetes*, and the *Galerita americana* and *africana* groups, have evolved independently a pattern of long, transversely aligned nodular microsculpture, and elongate sculpticells on the tops of the carinae.

Loss of carinae or carinulae has occurred independently in the *G. africana* group (carinae lost), and in the *G. americana* group (carinulae lost). Although these losses involve different structures, the end result in each lineage is similar.

Parallel development of macrosculpture and microsculpture.— As noted above, carinate macrosculpture has had correlated with it development of long narrow nodules, transversely arranged between intervals.

Significance of the Pattern

In order to highlight general implications of this study, brief comments are offered about historical, developmental, and functional significance of the evolutionary pattern of sculpture of the Galeritini. From an historical perspective, I suggest that the highly complex surface of the arthropod cuticle exhibits patterns of variation that are amenable to phylogenetic analysis. This study suggests that features of the cuticle are sufficiently stable that old patterns persist. For example, if the estimate of age of *Galerita* is correct (Ball, in press, based on vicariant distribution patterns of extant taxa), the subgenera of this genus pre-date the beginning of the

Tertiary Period, and the other genera likely originated still earlier. Therefore, the microsculpture patterns ought to be of a similar range of ages. Thus, seemingly minor and inconsequential details of surface structure have potentially as much value as have other, more obvious structural features for phylogenetic analysis and taxonomic use.

The examples of convergence are interesting, for they show that even rather complex and detailed similarities may arise independently. Thus, it is important to evaluate critically such similarities if one uses cuticular features in phylogenetic analysis.

Similarities between the patterns of evolution of macrosculpture and microsculpture exhibited among the species whose adults have carinate intervals may result from a functional relationship (see below) of genetically independent elements, or they may be the result of one system constraining the other. If these derived forms of sculpture were genetically independent of one another, then they would constitute separate character states for use in analysis of phylogenetic relationship. Perhaps, however, development of carinae somehow channels or influences development of the transverse pattern of and elongation of the nodules. If this is so, and if one wanted to use the characters as sources of evidence about evolutionary relationship, it would be necessary to determine the extent of the developmental relationship. If microsculpture type were totally dependent upon type of macrosculpture, then one would have but a single character, rather than two, with which to evaluate propinquity of relationship.

Previous authors (Hinton and Gibbs, 1969: 962; Lindroth, 1974: 261-263; Erwin, 1979: 547; Allen and Ball: 544; Goulet, 1983: 375; and Ball and Shpeley, 1983: 800) have considered the ecological role played by surface features of carabids, proposing that irregularities and dullness contribute to cryptic patterns, while brilliance caused by marked reflectivity or iridescence yields flash patterns which are confusing to potential predators. Alternatively (Erwin, 1979: 547), it has been proposed that since different patterns of sculpture are associated with different types of habitats, the patterns might function to protect an insect's body against unfavorable environmental influences. For example, a grated pattern (*i.e.*, diffraction grating) might be especially effective in shedding mud and water, and thus of value to insects living in wet, sticky environments. Using the analogy of a corrugated iron roof, the correlation of elytral carinae with longitudinally directed nodules looks like a run-off system for shedding unwanted material that comes in contact with the cuticle. Perhaps this system has therefore a similar function to that of a grated system of microsculpture, the different solutions being the result of selection for different types of environmental impediments.

More specifically, adults of *Eunostus* exhibit the transverse pattern of microsculpture. In other carabid taxa, this pattern is correlated with life in tightly-packed leaf litter, but I do not know if this is the type of habitat frequented by *Eunostus*. The nodular forms of microsculpture are characteristic of all other galeritine groups, whose range of habitats collectively extends from closed canopy rain forest to open woodland and riparian situations. So, the functional significance of the different types of microsculpture is not likely to be found by seeking correlates with different habitats. Correlation might be found at the level of microhabitats, when these have been determined for galeritines.

In spite of my inability to demonstrate its adaptive significance, since this evolutionary pattern has developed and has been maintained for an extended period of time, and since the features are exposed to environmental pressures including potential predators that rely on eyesight while hunting, it seems reasonable to infer that natural selection has influenced and is maintaining this structural system. Furthermore, in view of the rather small steps in at least portions of the transformation series, it seems reasonable to infer sustained directional

selection, perhaps associated with either changes in habitat, or with improved design for occupying the old habitats. (Ball, in press).

ANOTHER INTERPRETATION OF EVOLUTION OF ELYTRAL SCULPTURE IN THE GALERITINI

Reichardt (1967: 158) considered evolution of macrosculpture of the elytra of subgenus *Galerita*. Assuming that Subtype IVA sculpture was plesiotypic for this group, which he ranked as a genus, and to which he related *Planetes*, he proposed that Types I, II, and III and Subtype IVB were derived from the former Subtype: for II and IVB, by simple loss of carinulae; and for Types I and III, both by loss of the carinulae and reversion from carinate to costate or nearly flat intervals. In turn, this notion was based on two considerations: evident reduction of the carinulae in adults of highland species in Middle America, and association of this loss with brachyptery, an apotypic condition. However, he did not take account of the fact that associated with macrosculpture Types I and III is a plesiotypic form of microsculpture, nor that in the *G. africana* group (with Type II macrosculpture) there is no evidence that carinulae had ever been present.

Having taken account of these facts, and as well having shown elsewhere (Ball, in press) that the subgenus *Galerita* and *Planetes* are not closely related to one another, and consequently there is no need on the basis of out-group comparison to postulate that Subtype IVA macrosculpture is plesiotypic, I believe that Reichardt's hypothesis of the evolution of elytral macrosculpture in the Galeritini can be rejected.

CONCLUDING STATEMENT

In this paper, I have recognized and described the types of sculpture exhibited by representative galeritines, using both structural and phylogenetic considerations to do so. I have demonstrated a marked correlation between microsculpture pattern and the reconstructed phylogeny that I had made previously. Underlying the reconstructed phylogeny based on structural features, there ought to be a correlated series of ecological transformations. When the latter are found and analyzed, I believe we will have the basis for understanding in both functional and historical terms the patterns of evolution of elytral sculpture postulated here.

ACKNOWLEDGEMENTS

I offer thanks for the loan of especially important material for this study: to P. Basilewsky (Musée Royal de l'Afrique Centrale, Tervuren, Belgique), for making available a specimen of *Galerita perrieri* Fairmaire; and to D. H. Kavanaugh (California Academy of Science, San Francisco, California), for the loan of specimens of *Planetes* and *Eunostus*.

Technical assistance was provided by various members of the staff of my Department. D. Shepley and G. D. Braybrook collaborated in undertaking the work with the SEM. J. S. Scott did the layout and prepared the plates, which are vital components of this presentation. I. E. Bergum assisted with preparation of the final copy of the manuscript.

My associates R. S. Anderson and J. R. Spence reviewed a preliminary draft of the manuscript, and offered useful suggestions for improvement of presentation. Though I accepted most of their proposals and made extensive revisions, I declined to accept all of them. I am, nonetheless, grateful for their thoughtful, thorough reviews of both form and substance.

I must also acknowledge members of the audience at Hamburg, at the XVII International Congress, whose comments following my oral presentation, caused me to modify some of the statements that I made there.

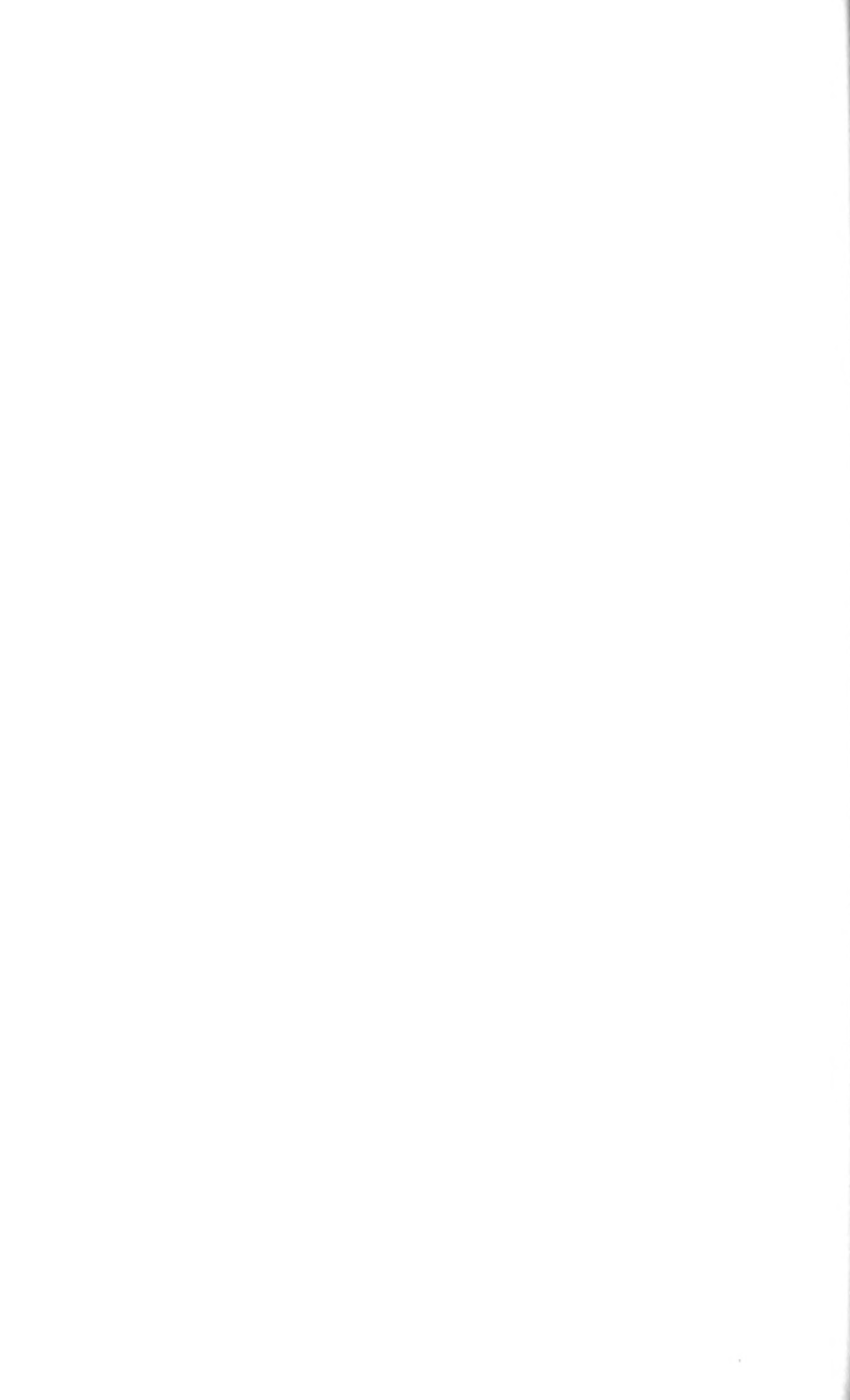
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I am very grateful for the generous and friendly cooperation that made this study a pleasure to undertake.

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BOOK REVIEW

D.C.M. Manson. 1984. Fauna of New Zealand; Number 4, Eriophyoidea except Eriophyinae (Arachnida: Acari); Number 5, Eriophyinae (Arachnida: Acari: Eriophyoidea). Science Information Publishing Centre, DSIR, Wellington, New Zealand. NZ \$10.50 (Number 4, 142 pp.), NZ \$9.00 (Number 5, 123 pp.).

These two volumes represent the first attempt at comprehensive systematic treatment of the Eriophyoidea of New Zealand. The author includes 109 species, of which 62 are recorded for the first time from New Zealand and 54 are new to science. The first volume (Number 4) deals with 49 known species listed in the families Sierraphytoptidae and Diptilomiopidae, and the subfamilies Cecidophyinae and Phyllocoptinae of the family Eriophyidae, while the second one (Number 5) includes 60 species of the eriophyid subfamily Eriophyinae.

In Number 4 the author begins with a brief introduction, followed by a useful historical review of the study of eriophyoid mites in New Zealand. He then discusses one of the most significant and controversial recent problems in the nomenclature of Eriophyoidea, and wisely opts to follow the ruling of the International Commission on Zoological Nomenclature concerning the retention of the pre - 1971 usage of the generic names *Aceria*, *Eriophyes*, and *Phytopus*.

The section on morphology is thorough and effectively introduces the reader to the terms used in the systematic sections. Unfortunately, the author has chosen to employ some very unusual concepts and inappropriate terms for describing certain acarine structures. For example, he refers to "three main body divisions - the rostrum, the dorsal or cephalothoracic shield, and the abdomen". In this case, "rostrum" and "abdomen" are imprecise terms apparently being used incorrectly in place of "gnathosoma" and "idiosoma", respectively, for the two generally-accepted, main regions of the acarine body. The dorsal shield is, in fact, simply a sclerite on the prodorsal region of the idiosoma. Other inaccurately applied terms, such as "claw" for solenidion and "featherclaw" for empodium, are used following the traditional but incorrect practices of many specialists on Eriophyoidea.

The next part, on the life cycle of eriophyoid mites, is a concise account outlining the so-called *simple* and *complex* types of life cycles in Eriophyoidea, and emphasizing the importance of recognizing the deutogyne form in species with the latter. This is followed by a comprehensive discussion of the different types of damage that various eriophyoid mites cause to host plants. The author notes that members of several species of Eriophyinae apparently, are regularly found associated with two or more distinct types of damage on hosts of the genus *Nothofagus*. As he points out, this finding suggests that the exclusive use of symptomatic damage to hosts in establishing the identity of eriophyoid mites, so prevalent in early works on the group, and still permitted by the International Code of Zoological Nomenclature, should be strongly discouraged.

The last 120 pages of Number 4, and all of Number 5, are devoted to systematic treatment of the fauna. Clear, straightforward keys and diagnostic descriptions are presented for the protogyne females of all taxa, providing an essential framework for future taxonomic work on the New Zealand fauna. A comprehensive set of fully adequate figures is included for each species, illustrating the diagnostic character states used in the keys and descriptions. Inexplicably, the author has chosen to use the family name Sierraphytoptidae for mites having 3 or 4 setae on the prodorsal shield even though the name Phytoptidae, with 67 years priority, is available.

Dr. Manson has admirably brought together existing information on the systematics of the Eriophyoidea of New Zealand, and these attractively produced volumes will be an important addition to the libraries of all students of the group.

Ian M. Smith,
Assitant Director,
Biosystematics Research Institute,
Ottawa, Ontario





Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at The University of Alberta in Edmonton in 1922.

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FAUNAL INFLUENCES ON SOIL STRUCTURE

Proceedings of a Symposium held at the University of Alberta, Edmonton, Alberta, CANADA,
June 11-13, 1984

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OIL, TOIL AND SOIL: An Introduction to the Symposium

The machinery of human interaction is facilitated by several lubricants, of which coffee is one of the most important in our society. Morning coffee break in the Department of Soil Science at the University of Alberta collected the people who conceived this symposium. On a cold day in November 1982, F. D. Cook, W. B. McGill, S. Pawluk, J. A. Robertson (all of the Department of Soil Science), H. V. Danks (Biological Survey of Canada (Terrestrial Arthropods)), and I warmed our fingers on pottery mugs and discussed common interests about soil arthropods around the table. A brief prepared by the Biological Survey of Canada (1982) drew our attention to the unexplored possibilities of opening dialogue between soil zoologists and pedologists in Canada. It was apparent that our understanding of soil arthropods in Canada was deficient. However, it appeared that we might know more than it seemed possible, if we could bring together people working on soil biology from quite different perspectives. We surmised that such a colloquium could contribute to assessment of needs and identification of priorities for soil biology in Canada. These became central objectives for organizing a soil animal conference.

After the creative dizziness of conception comes the toil of pregnancy and the ever present possibility of abortion. This is the pedestrian but onerous phase of organizing a conference. In this task, F. D. Cook, S. Pawluk and I were joined by N. Juma (Department of Soil Science) and J. A. Campbell (Alberta Environment, Research Management Division). V. Behan-Pelletier (Biosystematics Research Institute) was an adjunct member of this committee and contributed valuable advice and enthusiasm throughout the planning phase.

It is well known that soil animals contribute to soil function through effects on litter breakdown and nutrient cycling. However, we felt that the effects of soil animals on soil structure were less widely appreciated and because of our collective interests, we decided to focus the symposium on these interactions. Our nebulous "soil animal conference" became "Faunal Influences on Soil Structure". G. E. Ball (Chairman, Department of Entomology) and W. B. McGill (Chairman, Department of Soil Science) provided strong continuing support for our efforts and the Faculty of Agriculture and Forestry contributed seed money from the Endowment Fund for the Future.

As we developed the program, our concept of the symposium grew and we became most interested in attracting scholars of international reputation who might catalyse and contribute to the interaction between Canadian pedologists and soil biologists. At this point our squeaking wheels outran our budget and so we sought another important lubricant of human interaction - money. The response was generous and gratifying. We received financial support for the scientific program from the Natural Sciences and Engineering Research Council of Canada, Alberta Agriculture, Alberta Environment, The Alberta Research Council and the Canadian Society of Soil Science. Additional financial support from within the University community was provided by the Conference Fund Committee, Faculty of Agriculture and Forestry and the Departments of Entomology, Forest Science and Soil Science. The City of Edmonton and the Province of Alberta, respectively, agreed to host coffee breaks and the closing banquet with hospitality grants. We on the Organizing Committee are most grateful for this support.

The birth of this conference in June 1984 was more party than pain. About 80 participants representing ten countries arrived and three days of non-stop interaction followed. The prevailing spirit was that of a class reunion despite the fact that participants came from the two

rather isolated schools of soil zoology and pedology. It is a pleasure to acknowledge the assistance of H. van Blodeau and the staff at Lister Hall who arranged a pleasant and relaxed environment for the conference. S. Greenberg and V. Smyth of the Faculty of Extension organized and manned the registration desk assisted by several student volunteers.

The following collection of papers that were formally delivered at "Faunal Influences on Soil Structure" is but a pale reflection of what actually transpired. The Hon. F. D. Bradley (Minister of the Environment, Province of Alberta) and J. Gordin Kaplan (Vice-President (Research), University of Alberta) opened the conference by stressing the great potential significance of soil research in the contexts of agriculture and land management. The formal papers published or abstracted in this collection served as a starting point for the flurry of intellectual exchange that characterized the meeting. Many participants contributed posters summarizing their current work about animals in the soil. These and the workshop sessions were in a sense the heart of the conference and maintained a strong pulse of enthusiastic discussion.

It is our hope and belief that the record of this conference shall not end at the last page of this volume. Instead, we predict that a growing dialogue between pedologists and soil zoologists will lead to a new, more synthetic kind of soil science that includes soil biology at its core. There is much toil ahead but it should pay off handsomely in terms of applications and by increasing understanding of a fascinating part of the earth's biota. A central message of this conference is that these two objectives must travel hand in hand.

Finally, I wish to acknowledge the help and support of G. E. Ball who, in the capacity of editor of *Quaestiones Entomologicae* encouraged us to put this issue together and bore with us through the most difficult aspect of this project. We also thank S. M. Subbarao, publication manager for the journal, for her patience. Publication of these proceedings was made possible by support from the Endowment Fund for the Future of the Faculty of Agriculture and Forestry at the University of Alberta.

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ANALYTIC AND SYNTHETIC CONTRIBUTIONS

SOIL ZOOLOGY, THEN AND NOW – MOSTLY THEN

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Quaestiones Entomologicae

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ABSTRACT

Knowledge of the animals that inhabit soil remained fragmentary and virtually restricted to a few conspicuous species until the latter part of the 19th Century, despite the publication, in 1549, of the first attempt at a thesis on the subject by Georg Bauer (Agricola). Even the writings of far-seeing naturalists, like White in 1789, and Darwin in 1840, did not arouse interest in the field. It was probably P.E. Müller in 1879, who first drew particular attention to the importance of invertebrate animals generally in humus formation. Darwin's book on earthworms, and the "formation of vegetable mould", published in 1881, and Drummond's suggestions, in 1887, regarding an analogous role for termites were landmarks, but, with the exception of a few workers, like Berlese and Diem at the turn of the century, little attention was paid to other animals in the soil, save incidentally to other investigations. Russell's famous Soil Conditions and Plant Growth could say little about the soil fauna other than earthworms. Prior to the Second World War, Bornebusch, in 1930, and Jacot, in 1936, attempted to broaden the horizons of both zoologists and pedologists, but it was not until the end of the war years beginning with Forsslund's work in Sweden, published in 1945, that soil fauna studies really got under way. From the pedological, rather than the zoological point of view, a book by Kubišna, published in 1948, set the stage. Then, in addition to research publications, several books on different aspects of soil fauna in general appeared from 1949 to 1951 by: Gilyarov, Franz, Kühnelt, and Delamare de Boutteville. The first international colloquium on soil fauna was held in 1955, since when there have been many, the latest before the present one in 1982. There has nevertheless (with a few notable exceptions) been a general lack of interest in the fauna on the part of pedologists, and reluctance to intrude into the realms of so-called "soil science" by soil zoologists, to mutual disadvantage. There is still an almost complete absence of appreciation, especially among those who determine the directions of soil research, that we are still without the means of proper identification of innumerable members of the soil fauna, and that the understanding of basic soil ecology and the pedological importance of the fauna is impossible without this.

RÉSUMÉ

L'auteur passe en revue le développement des connaissances sur les animaux qui habitent dans le sol, depuis les débuts jusqu'à maintenant. Ces connaissances demeurèrent fragmentaires et pratiquement restreintes à quelques espèces frappantes jusque dans la deuxième moitié du XIX^e siècle, et ce malgré la parution, en 1549, d'un premier essai de

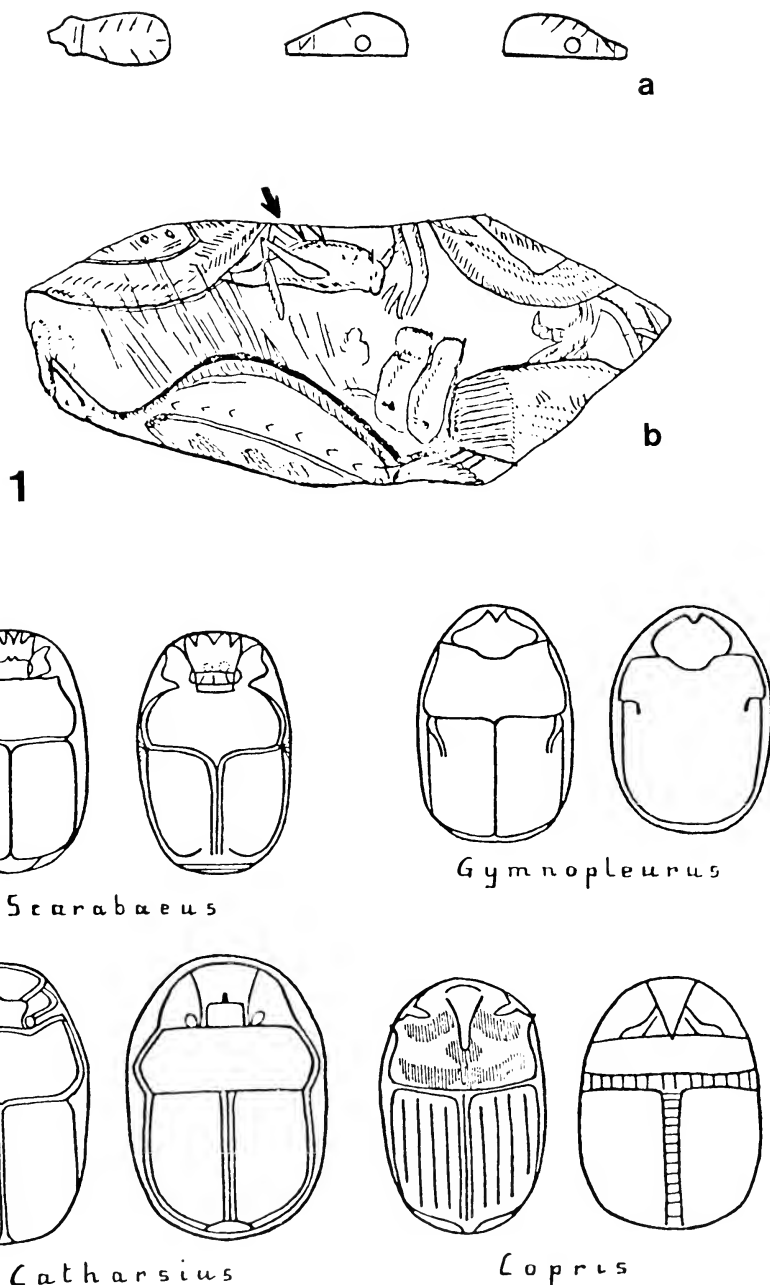
thèse sur le sujet par Georg Bauer (*Agricola*). Même les écrits de naturalistes clairvoyants, tels que White (1789) et Darwin (1840), n'émulèrent que peu d'intérêt dans ce domaine. P.E. Müller (1879) fut probablement le premier à porter une attention particulière au rôle important des invertébrés dans la formation de l'humus. L'ouvrage de Darwin (1881) sur les vers de terre et «la formation des moisissures végétales» et les suggestions de Drummond (1887) concernant un rôle analogue chez les termites constituèrent des événements marquants, mais, à l'exception de quelques chercheurs tels que Berlese et Diem à la fin du siècle, la plupart portèrent peu d'attention aux autres animaux vivant dans le sol, sauf accessoirement durant le cours de d'autres travaux. Le fameux ouvrage de Russell paru en 1912 et intitulé *Soil Conditions and Plant Growth* contient peu d'informations sur la faune des sols autre que les vers de terre. Avant la Deuxième Guerre Mondiale, Bornebusch (1930) et Jacot (1936) essayèrent d'élargir les horizons des zoologistes et des pédologues, mais ce ne fut qu'à la fin de la guerre que l'étude de la faune des sols prit vraiment son essor avec les travaux de Forslund en Suède en 1945. Du point de vue pédologique plutôt que zoologique, l'ouvrage de Kubiëna (1948) établit le domaine. Par la suite, en plus d'articles scientifiques, plusieurs ouvrages traitant de différents aspects de la faune des sols en général parurent en succession rapide: Ghilarov (1949), Franz (1950), Kühnelt (1950) et Delamare de Boutteville (1951). Le premier colloque international sur la faune des sols eut lieu en 1955 (Kevan, 1955) et fut suivi par plusieurs autres, dont le dernier précède celui-ci eut lieu en 1982 (Lebrun et al., 1983). Néanmoins, on remarque en général un manque d'intérêt dans la faune des sols chez les pédologues (mis à part quelques exceptions notables), de même qu'une hésitation de la part des zoologistes étudiant la faune des sols à s'ingérer dans le domaine des soi-disant «sciences des sols»; cette attitude constitue un désavantage mutuel. Il existe un manque quasi total d'appréciation, particulièrement chez ceux qui décident de l'orientation de la recherche sur les sols, du fait que nous ne disposons toujours pas d'outils adéquats pour identifier les innombrables membres de la faune des sols, et que notre compréhension des éléments de base de l'écologie des sols et de l'importance pédologique de la faune ne pourra s'améliorer sans cela.

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INTRODUCTION

Prehistoric man was well aware of other creatures that shared his environment, and he undoubtedly associated some of these, such as various "worms", ants and termites with the earth beneath his feet. Like his present-day counterparts among the Bushmen of southern Africa and the Aborigines of Australia, too, he probably obtained an appreciable part of his food by digging for insect grubs. Nevertheless, the nearest thing, of which I am aware, to direct evidence for this acquaintance with such humble creatures is what seems to be a presumed amulet in the form of a possible *Necrophorus* burying-beetle of the Magdalenian culture of southern Germany, some 25,000–30,000 years ago (Peters & Töpfer, 1932; Schimitschek, 1977)(Fig. 1a). Another representation of a subterranean insect (though of a cave-, not a soil-inhabiting one) is also from the Magdalenian culture, but from southern France and



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Fig. 1. Artifacts from the Magdalenian culture of Europe. (a) The oldest known representation of an insect, probably a *Necrophorus* burying-beetle; amulet made of Tertiary carbon from Hegau, Baden, Germany, 25,000 to 30,000 years old; after Peters and Toepfer (1932). (b) *Troglophilus* camel-cricket scratched on bison bone, Caverne des Trois Frères, Ariège, France, some 20,000 years old; after Bégouen and Bégouen (1928). Fig. 2. Ancient Egyptian stylized scarab seals (right member of each pair, various dates), compared with actual insect sketched on ovals (left member of each pair). After Petrie (1917).

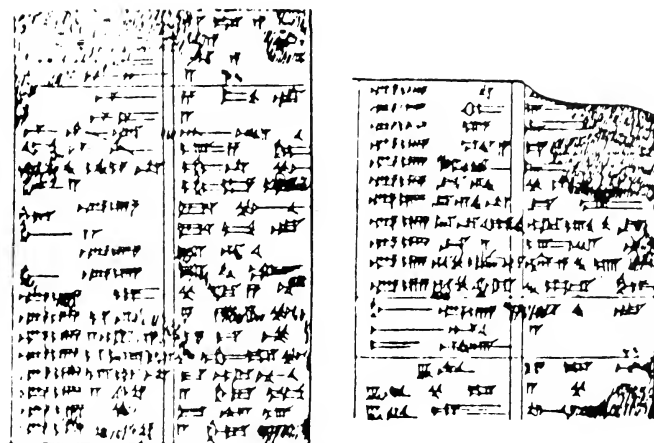
apparently of considerably later date, though probably some 20,000 years old. This is in the form of a picture, scratched on a bison bone, clearly representing a species of the camel-cricket genus *Troglophilus*, which does not now occur in the region (Bégouen & Bégouen, 1928; Chopard, 1928; Schimitschek, 1977)(Fig. 1b). I know of little if anything else which antedates the ancient civilizations of Near, Middle and Far East that is relevant to our present theme.

THE ANCIENT WORLD

From very early times (though there is little direct evidence from earlier than the 3rd Millennium B.C.E.), scarab beetles were revered, depicted and modelled in Egypt as symbols of Khêper (Fig. 2), a manifestation of the all-powerful Sun-god, Rā or Re (see, for example, Newberry, 1905; Petrie, 1917; Bodenheimer, 1928, 1949, 1960; Efflatoun, 1929; Schimitschek, 1968, 1977; Harpaz, 1973). It is thus unlikely that the priestly class was entirely unaware of the biology of such important creatures, parts of whose lives are intimately associated with soil. Nevertheless, so far as I can discover, and despite implications repeated by Harpaz (1973) to the contrary, there seems to be no written record of anything that may have been known at the time (with or without religious or philosophical association), other than what the adult beetles looked like and that they rolled dung-balls (Bodenheimer, 1928, 1949, 1960). Whether "worms" attacking ancient Egyptian crops were specifically cutworms (e.g., *Agrotis ypsilon*), as suggested by Efflatoun (1929), is a moot point.

We can infer from ancient sources, dating back to the 2nd Millennium B.C.E., that cicadas have been known from time immemorial to be part-time denizens of the soil, emerging in "ghostly" or "spiritual" form, as from the grave, symbolizing, notably in China, purity, immortality and/or resurrection after death (Brentjes, 1954, 1964; Schimitschek, 1968, 1977; Kevan, 1978; Riegel, 1981). They also had less lofty significance in "magic" and medicine and (as nymphs) as food (Chou, 1980; Riegel, 1981). The ancient Hellenes later, ultimately from the east (H. Kühn, 1935; Brentjes, 1954, referring also to two other publications by Kühn from 1943), acquired a reverence for cicadas. Especially among the people of Attica and Ionia, these insects came to symbolize an almost religious bond between man and his native soil. This sacred significance did not, however, preclude cicada nymphs from being dug up in large numbers by the ancient Greeks and used as food, as they were in China (cf. Kevan, 1978: 28, 29, 42, 45, 49). The oft-cited Athenian hair-ornaments called *têttiges* (i.e., cicadas) were probably based, if any actual insects were involved, upon soil-dwelling nymphs and not on winged adult cicadas (certainly not on grasshoppers as misguided western tradition has it!). This topic has been briefly discussed fairly recently by Kevan (1978: 435–436), but see also Hauser (1906–1908) and Brentjes (1954, 1958). Probably of similar antiquity to the Old World tradition, though without tangible evidence of this, are the Amerindian legends of both cicadas and ants being among the first creatures to emerge through the soil from the centre of the earth to populate its surface (see Kevan, 1983b). The soil fauna is thus something that has always been of interest to civilized as well as to primitive man.

Although legends and artifacts form a significant part of our source material relating to early knowledge and belief, we tend to place greater emphasis on the written word. In this regard, other than the earliest ancient Egyptian hieroglyphs for scarab beetles, and at least as old in written origin (though not in existing writing) as some of these, the earliest known references relating to our theme are those of the ancient Sumerians of present-day southern Iraq. Some 4,000 or more years ago, at the very latest, these enlightened people were certainly

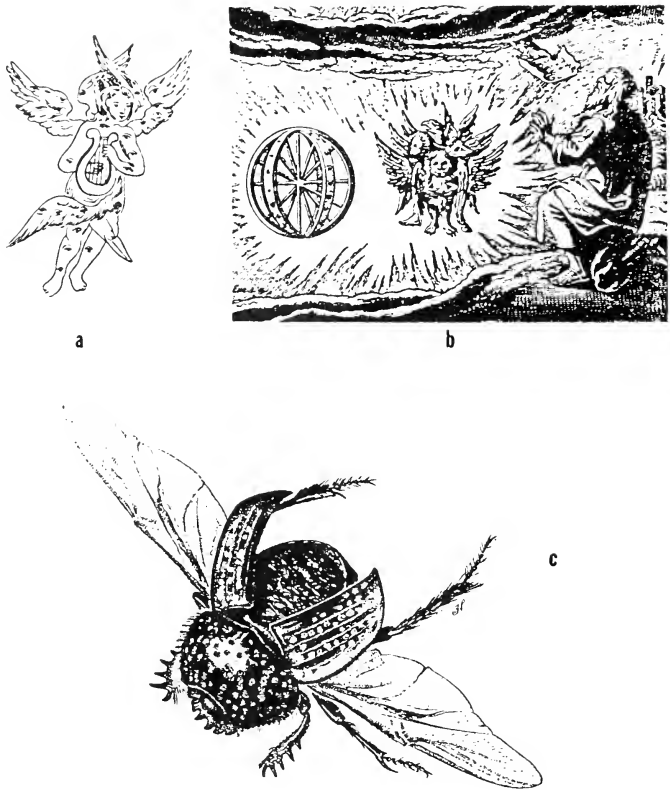


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Fig. 3. Fragments from the ancient Sumerian-Akkadian zoological lexicon, the *Harra-Hubullu* - see below. After Bodenheimer (1949).

familiar enough with various members of the soil fauna to have applied different generic and specific (binominal) names to a number of them *and to have written these down*. Of such names we know a few from the *Harra Hubullu*, a compendium prepared in the 9th Century B.C.E. by the successors and neighbours to the Sumerians, the Akkadians, giving equivalents in the two languages (Landsberger and Krumbiegel, 1934; Bodenheimer, 1949, 1960; Harpaz, 1973)(Fig. 3). The Sumerians of the early 18th Century B.C.E. (the time relevant to the later Akkadian text), and probably much earlier, distinguished between at least seven kinds of ants or *Kiši* (including *Kiši ririga*, or flying ants, and *Kiši kurra*, light-coloured and perhaps termites, not ants) and two kinds of earthworms of the annelid genus *Mar*, the *Mar gal* (or *Mar dib*) or *Mar tab* and *Mar šasur*. They also had binomina for what seem to have been a mole cricket (*Gryllotalpa*), which they called *Ub pad*; for (field) crickets, known as *Buru zapâag(-tira)* or *Buru balag(-gana)* (*Buru* being the generic name for orthopteroid insects); and for a small, self-burying orthopteroid named *Buru saħarra*, or "dust locust" (which, very tentatively, I have identified elsewhere as the pyrgomorphid *Tenuitarsus angustus* (Blanchard)).¹ What the Sumerians or Akkadians knew about these animals, however, we have no idea, though we can surmise that the former probably knew much more than history or archaeology will ever reveal. After all, in the fifth part of their most ancient of epics, the "Flood" legend of Gilgāmesh, they apparently associated adult dragonflies with the moulting of their aquatic nymphs (Sandars, 1959) thousands of years (so far as we are aware) before anyone else did so.²

Not quite so ancient as Sumerian sources are the early Sanskrit Vedic books of late in the 2nd Millennium B.C.E. These refer not infrequently to ants and/or termites, as indicated by various verse quotations given by Kevan (1978), though, apart from an association with subsurface moisture in two examples, the references are little related to soil.³ Kevan (*op. cit.*) also gives later examples from early literature (including old Tamil, or Sangam, and later Sanskrit) relating to ants and termites, but mention of their role in the soil is again minimal.



4

5



Fig. 4. "Ezekiel's wheels" (see text). (a), (b) Artists' fanciful interpretations of Ezekiel's cherubim; (a) after G. Eicke, 1964, in Schimitschek (1968); (b) after W. Merian, 1650; for reference, see Hogue (1983). (c) *Scarabaeus cicatricosus* in flight, showing salient features compatible with Ezekiel's account; after Hogue (1983). Fig. 5. Chinese mole cricket, *Gryllotalpa orientalis*, from the ancient illustrated encyclopaedia of Pu Shang, the *Erh-Ya*; from a late printed edition of about A.D. 1600. After Bodenheimer (1928).

The allusions to cicadas and ants in early Hellenic literature of the Homeric and immediately subsequent periods (9th-8th Century B.C.E.) are likewise mostly unrelated to the soil, and it is only in considerably later works that we come across surviving references to their "earthly" associations (see Bodenheimer, 1928, or, more briefly, Morge, 1973).

Although much Israelitic tradition is very ancient, most of the Hebrew scriptures as we know them, with some exceptions, were written down no earlier, and often much later, than the 6th Century B.C.E. These Scriptures, though referring quite frequently to insects, make virtually no unequivocal references to the soil fauna (the allusions to ants, in Proverbs VI, 6, and XXX, 24-25, being near exceptions).⁴ Such references as there are to "worms" (*tola'ath*), where epigeic, plant-feeding insect larvae are not involved, are almost invariably to flesh-feeding dipterous maggots. Bodenheimer (1928, 1929, 1960) reviews briefly the insects referred to in the Hebrew Scriptures. There is, in addition, one brief reference, in the Book of Micah, VII, 17 ("King James", 1611 version: "... like crawling things of the earth they shall come trembling out of their close places ...") that might conceivably refer to earthworms (indeed an alternative translation uses "worms ... move"). The principal interest of this uninformative passage lies in its possible antiquity. The book in question probably dates from about 720 B.C.E., though its later sections (including Chapter VII) could well be by a later author.⁵

Much more intriguing, on account of its controversial nature, is the somewhat later book of the prophet Ezekiel, originally dating from about 590 B.C.E. The Egyptian scarab cult, to which reference has already been made, eventually became widespread in the Near and Middle East, including Babylonia, where Ezekiel, like other Israelites of note, was captive. It is possible that, being a priest, he studied these religiously important insects out of interest, if not conviction. It has been concluded (Sajó, 1910; Schimitschek, 1968; Hogue, 1983) that he gave them the name *cherubim*, couching his description (made, probably, in the glaring sun) in allegorical, pseudoreligious terms (as would befit such venerable creatures) to the subsequent (possibly intentional) mystification of all and sundry (Fig. 4a, b). If an entomological interpretation of Ezekiel's *cherubim* be accepted, however, there is little in his account that goes much beyond the identification and description of the scarab beetles (Fig. 4c) and their dung-balls, though there is a hint of something more (Hogue, 1983).

In the 5th Century B.C.E., about a century after Ezekiel was allegedly peering myopically at scarabs by the Chebar canal in Babylonia, the Chinese illustrated encyclopaedia of Pu Shang, known as the *Erh-ya*, made its first known appearance (to be followed by numerous editions throughout the centuries). In it, soil fauna, including mole crickets (Fig. 5), scarabaeoid beetles (and their dung-balls and larvae), ants of several kinds, cicadas and centipedes were all included (Bodenheimer, 1928, 1929), though how many of these were in the "first edition", I do not know. So far as I can tell, little was included on the direct soil association of any but the mole crickets and cicada nymphs. Other ancient Chinese literature, e.g., in the form of early "herbals" or *pên-ts'ao*, is referred to by Chou (1957, 1980) and Konishi & Itô (1973), but the soil fauna is scarcely considered.

Although there were a number of early Hellenic literary references to insects and other terrestrial invertebrates (see, for example, Bodenheimer, 1928; Morge, 1973; Kevan, 1978), virtually none of the surviving writings mentioned soil-inhabiting animals, with the exception of brief allusions to gigantic, subterranean gold-digging "ants" in "India", which eventually became the mythical "ant-lions", and a hateful, biting creature known as the *amphisbaina* (amphisbaena). The latter, mentioned by Aiskhúlos (Aeschylus, 5th Century B.C.E.) in his

Agamemnon (see Druce, 1910), was traditionally (from later sources) a two-headed, poisonous burrowing serpent. Of both of these denizens of the earth, more will be said later, but it may be noted here that the giant ants are mentioned in the *Historiēs Apódexis* of Hēródotos Halikarnēseos (Herodotus) of the mid 5th Century B.C.E. (Rawlinson, 1910). Quatrefages (1854) suggested that large termite mounds, rather than ant-hills, provided a basis for the legend. Hēródotos also mentions, in passing, the underground activities of Greek ants, but it was not until the time of Aristotēles Asklepiádos (Aristotle) that we have anything approaching scientific observation.

Of Aristotēles' five "notebooks" on zoology of about 320 B.C.E., four, now known by their Latin titles of *Historia Animalium*, *De Generatione Animalium*, *De Partibus Animalium* and *De Incessu Animalium*, the original Greek texts being long since lost, mention a few soil-dwelling creatures (see D'A.W. Thompson, 1910; Platt, 1910; Ogle, 1911; Farquharson, 1912). Though western scholars have, for centuries, been "brainwashed" into accepting Aristotēles as the founder of biology, he was really a late-comer, if an extremely important one, to the scene. His contributions to various aspects of the science were undoubtedly of immense significance, but he may well have transmitted many ideas from already ancient Middle Eastern (or even Oriental) sources of which we have no record. (One can scarcely imagine that the Sumerians, for example, did not bring about the dissemination of valuable zoological information). For all his great erudition and commendable powers of observation, Aristotēles contributed surprisingly little knowledge of the soil fauna (see the short entomological review by Bodenheimer 1928, 1929, and the even shorter one by Morge, 1973, based upon it). Indeed he had some very peculiar ideas on mould, decay and humification. With great originality (!) he observed (*Historia Animalium*, I, 1), that "some creatures dwell under ground, as the lizard and the snake." (he had just mentioned that some provide themselves with homes, including mole and ant, so he did not immediately cite these again as examples); other versions of the text read: "some make themselves holes; others not so" (D'A.W. Thompson, 1910). He gave a reasonably good, succinct description of the life-history of cicadas, including the subterranean nymphal stage, or *tettigometra* (which he pronounced to be good to eat), and he also gave some notes on the biology of scarab beetles (*kántharoi*) and their dung-balls, and on the life of ants. Other soil fauna which he briefly described were myriapods, earthworms ("γῆρ emseqa or "earth's entrails") and moles. Both millipedes and centipedes were said to remain active after being cut into pieces (though there seems to be some confusion here with their marine, annelid-worm, counterparts). His two main references to earthworms were oddly confused with the origin of eels. Moles, he stated, cannot burrow if they are transported from one location to another. Aristotēles also mentioned certain "marginal" soil animals: woodlice, scorpions, pseudoscorpions, mites on insects (Oudemans, 1926), and digger wasps, burrowing bees and bumblebees. He did not mention the amphisbaena. His disciple Theophrastos, though making valuable contributions to entomology in the course of his botanical studies, did not refer to subterranean insects except for (cut)worms (?) that attack both roots and stems of wheat. Later, we have the opinion of Kleanthēs, about 270 B.C.E., that ants behave only instinctively - though Plutarch, about 100 A.D., believed later that they reacted intelligently (see Bodenheimer, 1928; Morge, 1973). Shortly before 200 B.C.E., the Roman playwright Titus Macchius Plautus (in *Mostellaria*, III, 2) refers to "*tarmes*" (some kind of wood-feeding insects, conceivably termites) boring from below ground (Kevan, 1978: 425).

The Macedonian physician Níkandros (Nicander) of Kolophōn, in his *Thēriakos* and *Alexipharmakos* of about the mid 2nd Century B.C.E., wrote extensively (in verse) on animals,

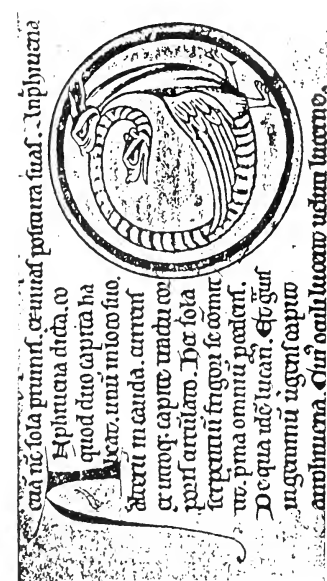


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Fig. 6. The dreaded, two-headed, subterranean Amphisbaina (see p. 375): illustrations from Byzantine manuscripts descended from Nikandros' *Theriaka* of 2nd Century B.C.E., taken from Kádár (1978 : pl. 8, 55, 101). Top, from Cod. Paris. Suppl. Gr. 247, 10th Century; middle, from Cod. New York Pierpoint Morgan M. 652, 10th Century; bottom, from cod. Bonon. (Bologna) Bibl. Univ. Gr. 3632, early 15th Century.

without knowing very much about his subject. He had much to say about serpents and scorpions, and, with reference to the former, there is, in *Thēriakos*, a formula for utilizing the skin of the abhorrent amphisbaena against various maladies (cf. Druce, 1910; Kevan, 1978; 63, 444; the latter gives a fragment of the Greek original with a somewhat "unorthodox", inaccurate English translation from a Latin version). Much the same is given (in prose) by his approximate contemporary, Apollodōros of Athens, in his *Bibliothēka*, and it would seem likely that this was Nikandros' immediate source. The rather small, poisonous, half blind underground serpent (Fig. 6), with a head at each end and the capacity to progress in opposing



7



8

Fig. 7. Mediaeval concepts of the "Amphisbena" or "Amphivena" (1). From Anglo-Latin "Bestiaries" in the British Museum Library, London (after Druce, 1910). Above, from MS Harley 4751, late 12th Century (there is a similar example, MS 764 fol. 97, in the Bodleian Library, Oxford); below, from MS Harley 3244, early 13th Century. Note: in both examples the creature has sprouted wings and two legs (in which it resembles a Basilisk or Cockatrice) and it is no longer soil-dwelling: the upper figure indicates one mode of progression adopted – by seizing the posterior neck in the anterior jaws and rolling like a hoop! Fig. 8. Mediaeval concepts of the "Amphisbena" or "Amphivena" (2). From ecclesiastical architecture and furniture (after Druce, 1910). Above, pillar capital, Freising Cathedral, Bavaria (? 13th Century), showing simple, wingless apodous, "Satanic" form of the beast biting the arm of Eve (?), left (from Cahier and Martin, *Mélanges d'Archéologie*); below, carved misericord, Limerick Cathedral, Ireland (? 14th Century), sophisticated form as in Fig. 7.

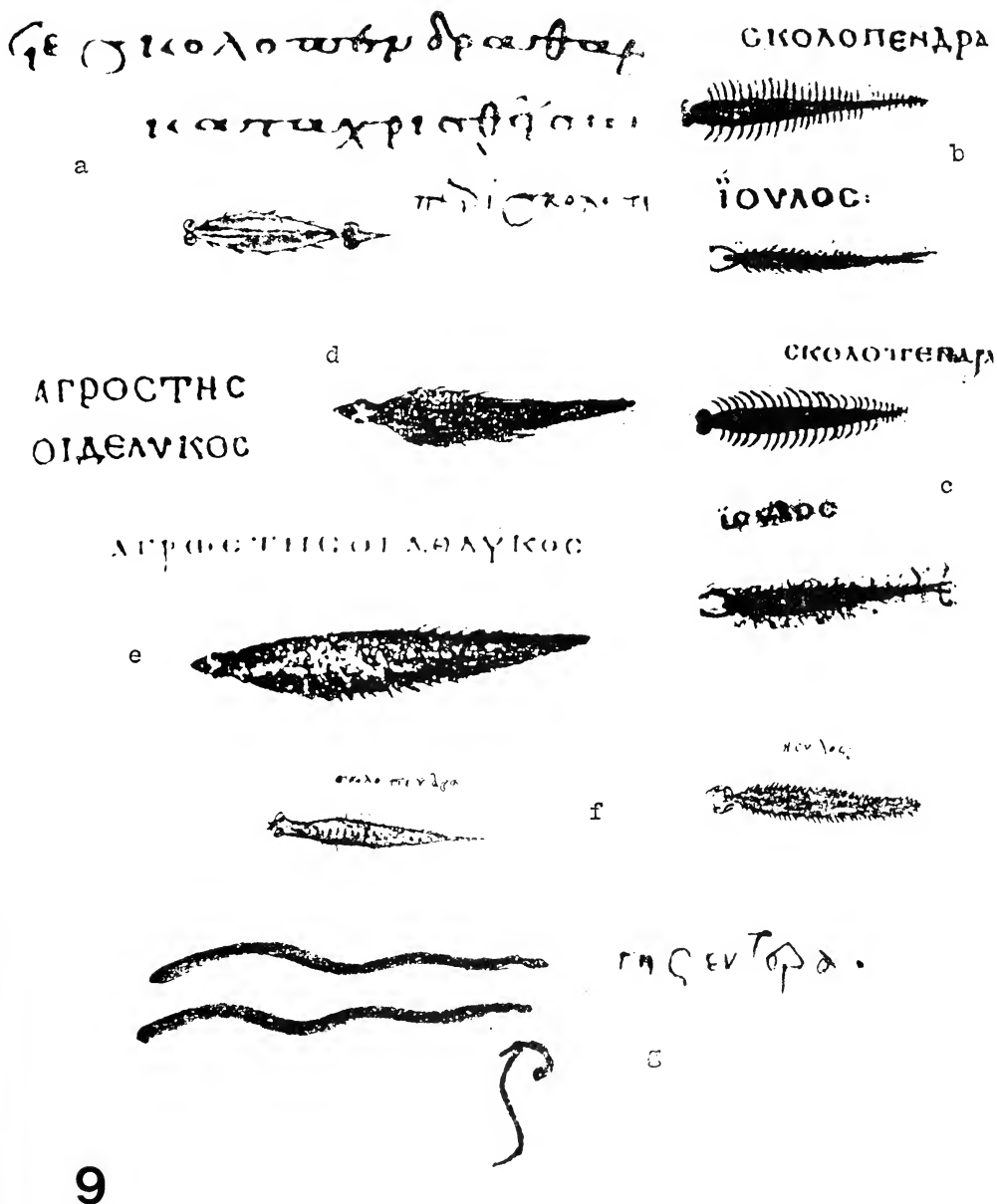
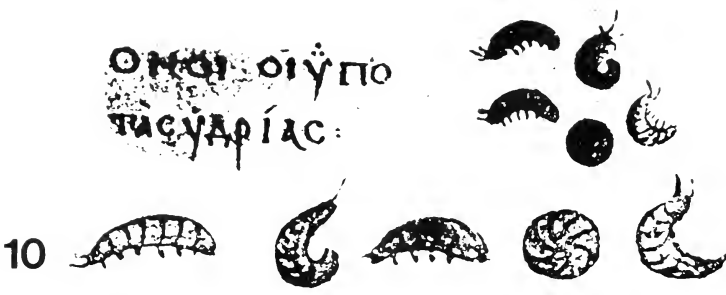


Fig. 9. Illustrations of myriapods and worms from Byzantine manuscripts descended from Níkandros' *Theriaka* and *Alexipharmakos* of 2nd Century B.C.E., and from Dioscorides' *Pharmaka* of 1st Century A.D., taken from Kádár (1978). (a) *Skolopendra* (centipede), from Cod. Vatican. Gr. 284, 10th Century; (b) *skolopendra* and *ioulos* (? millipede, possibly marine polychaet worm), from Cod. New York, Pierpoint Morgan M. 652, 10th Century; (c) the same, from Cod. Vindobon. (Vienna) Med. Gr. 1, ? 10th Century; (d) *agrostēs hoi de lukos* (possibly a polydesmid millipede, but may be modelled on a marine polychaet worm), same source as (b); (e) the same, same source as (c); (f) *skolopendra* (centipede) and *ioulos* (millipede), from Cod. Bonon. (Bologna) Bibl. Univ. Gr. 3632, early 15th Century; (g) *gēs entera* (earth's entrails, earthworms), same source as (a), name transposed from above worms.



Theobaldus
De naturis animalium

Et postq̃ p̃ malam suggestionem deceptus fuit accessit eū ⁊ momos
dit ipm p̃ peccā. Sic diabolus antiqu⁹ serpens hominē nudū a pec
catis ⁊ cōsulatū a vitis fugit. et vestitū peccatis ledit inq̃rū p̃t mor
et eterna. Nā p̃pterea dē auro: sicut radj solares fugant vmbrositatez
noctis. simili modo hō mūdus a peccatis fugat a se demonē. aramen
oportet ipm adhuc habere pugnas ⁊ diuersas t̃bulatōes per totam
vitam suā. tanq̃s homo certans in agone. Unde iob. Miliria est vita
hominis super terram. Et alibi. Qui legatime certauerit coronabit.
Item serpens totū corpus suū exponit l̃sioni vt caput obrineat ill
l̃cium ad finem ne moriat. Simili mō debet ⁊ vitis tenet vnusquisq̃
christianus totam vitā temporalem exponere pro capite. id est p̃ chri
sto. Unde christus est omnū christianoz caput. ⁊ christiani econtra
sunt membra ipsius. Si ergo aliquis vellet impugnare fidem chri
stianā. homo christianus deberet exponere totū corpus pro ea. ⁊ potius
mori q̃ christū denegare. Vnde cū sanctorum mortui sunt pro fide
christiana. sed eternā receperūt retributiōem. Nota q̃ adhuc s̃s alie
nature serpentis. q̃s p̃bs in libris de aialibz recitat. Quaruꝫ vna est q̃
serpens habet linguā diuisā ad modū duoz digitorū. Ad sic exponi
tur allegorice. Aliqui sunt homines duas linguas habentes. qui scz in
p̃sencia aliquoz loquunt bona: ⁊ in absentia eorū dē de ipsis loquunt
mala detractorie. ⁊ isti bilingues veluti serpentes vitandi ⁊ fugandi
sunt. nec in aliquo credendi. Item alia natura serpentis est. scz q̃ qñ
aliquis dormit in campo aperto oze. ruc serpens intrat os illius. Qu
tus ratio est. quia serpens frigide est nature: ⁊ anhelitus hominis est
calidus. ergo q̃tum potest nutritur appropinquare anhelitui hominis
⁊ sic os apertum inueniens ipsum intrat. Sic boni ues aliqui quando
audiunt aliquem predicantem aut docentem. in verbis ipsius euz ca
piunt reprehendendo verba sua

De formica

Et modū viuēdi dat
Exemplum nobis prebet formica laborio
sum p̃suetū genit
Quando suo solitū portat in ore cibum
gestis denotat
Inq̃ suis factis res monstrat spirituales
s̃ res diligit (deo
Quas (quia iudeus non amat). inde reus
Ut valeat bene fieri secunda future
s̃ est s̃ formica
Dum calor in terra non requiescit ea

11

b f

Fig. 10. Illustrations of (presumably) the isopod crustacean *Armadillidium vulgare* (*Onoi hoi hypo tās hydrias*) from 10th-Century Byzantine manuscripts descended from Dioskorides' *Pharmaka* of 1st Century A.D., taken from Kádár (1978: pl. 72, 89). Above from Cod. New York, Pierpoint Morgan M. 652; below from Cod. Vatican. Gr. 284. Fig. 11. Part of the account of the Ant from a late metrical version of the *Physiologus* attributed to Bishop Theobald of Monte Cassino, early 11th Century. From the printed version, *Physiologus Theobaldi Episcopide naturis duo decim animalium*, Köln, 1492 (see Rendell, 1928).

directions (simultaneously ?!), seems to have been known and feared since before the time of Aiskhúlos and Hēródotos, though Níkandros did not mention its venom, or its mode of progression. It was probably based originally on the harmless burrowing, worm-like reptile we now call *Trogonophis* (the related modern genus *Amphisbaena* is tropical), rather than on the blind-snake, *Typhlops*, which was also known at the time.⁶

Níkandros also made various references to insects, though nothing definite was said about their relationships with the soil. Judging by Byzantine illustrations (Fig. 9), copied from generation to generation (see Kádár, 1978), he seems to have known, in the Aristotelean tradition, about centipedes (*skolopendra*) and possibly millipedes (*íoulos*), though both may more usually have been (? marine) annelids. (With reference to the latter, see discussion of a Greek 2nd Century A.D. poem by Neumenios, in Kevan, 1978: 334). Kádár (1978) indicates that another, later and much better-known physician, active in the middle of the 1st Century A.D., Pedanios Dioskoridēs, also knew of some soil animals, such as earthworms and the others referred to by earlier authors, including Aristotēles and Níkandros (Fig. 9, 10). These he listed in his *Pharmaka* (*De Materia Medica*). Woodlice of the genus *Armadillidium* (presumably) were apparently known to him as *onoí hoy hypo tās hydrias*. In the 1st Century also, the poet Marcus Annaeus Lucanus (Lucan, 39–65 A.D.) emphasized the venomousness of the burrowing amphisbaena in his *Pharsalia* (see Druce, 1910).

The Aristotelean tradition, somewhat embellished, was carried on by the Roman Gaius Plinius Secundus, or Pliny the Elder (77 A.D.; see Rackham, 1940). Though a great compiler, he was unoriginal and often gullible. In his *Naturalis Historia*, he had little to say (and nothing new) about the soil fauna, though he did mention cicadas (including their subterranean *tettigometra* nymphs) and scarabaeoid beetles. He also seems to have been responsible (after Strabōn, or Strabo, in his *Geōgráphikos* of 23 A.D.) for “popularizing” the early myth of the fabulous, gigantic, dog-like, gold-digging “ants” of “India”, to which reference has already been made (see above, and George, 1981). The “ant-lion” (*myrmēcoleōn*, later *mirmicoleon*, etc., sometimes also called “ant-dog”) made its way into early versions of the symbolic Christian *Physiologus* (below and cf. Fig. 12), to which the lost 2nd-Century Greek *Peri Zōōn* of the Syrian monk Tationos may also have contributed.

“*Physiologus*,” or “The Naturalist,” was presumably originally the pseudonym adopted by, or for, an unknown compiler of the book that bears the name. The latter originated in the eastern Mediterranean (Alexandria or Syria ?), probably towards the end of the 1st or in the early 2nd Century A.D., but the Christian *Physiologus* perhaps came a century or so later. Extant material goes back to about the 5th Century (James, 1928; Rendell, 1928; Bodenheimer, 1928; McCulloch, 1962; George, 1981). It was copied in several versions and eventually led to the Mediaeval “Bestiaries” (*Libri Bestiarum*). The earliest Greek versions included 63 chapters, of which 56 were devoted to different animals (C. Peters in Bodenheimer, 1928; Morge, 1973). Of these, only the ant, the “ant-lion” and the scarab concern us here. The second of these, though fabulous as presented, and having mythical attributes, had, like other strange animals in the *Physiologus*, a basis of factual existence.⁷ As explained by George (1981), this was probably the badger-like ratel (*Mellivora capensis*), which burrows in sand and soil, though the pangolin (*Manis*) had been considered previously to be a likely candidate (Rawlinson, 1910, and others noted by George, 1981).

Before concluding our brief review of the so-called “classical” period of the Western World, we should perhaps note that there were various other works that had a bearing on applied entomology, from Cato, 235 B.C.E., to Palladius, ca. 380 A.D. (Bodenheimer, 1928; Morge,

1973). Although virtually none have any direct relation to the present context, we should perhaps mention the account of field crickets given by Publius Nigidius Figulus, mid 1st. Century B.C.E., in his *De Animalibus* (cf. Wotton, 1552; Bodenheimer, 1928), as this was distorted much later by Rhabanus Maurus (see p. 384?). Field crickets burrow backwards in the soil (and chirp at night); they may be hunted by inserting an ant on a hair, blowing away the dust the while; they can then be dragged forth together with the ant [which clings to it. Greek references to catching crickets in much the same way, by means of a strand, go back much further into antiquity.] Collumella, ca. 50 A.D., mentions ants, snails and miscellaneous caterpillars. Aelianus, about 200 A.D., dispensed numerous moral tales involving animals, including ants in particular, but also the "ant-lion" and amphisbaena, but these had not even a pseudoscientific significance. Gaius Iulius Solinus, in his *Collectanea Rerum Memorabilium* (later *Polyhistor*) of the second half of the 3rd Century, transferred the ant-lion from India to Ethiopia. He also maintained that the amphisbaena had two heads.

In the Orient, this late classical period of the Occident was not particularly notable for known observations on soil-inhabiting animals, though, in China, there was, as in the West, a keen interest in "herbals", or *pên-ts'ao*, which included medically important insects. The earliest proper pharmacopoeia, the *Shen-nung Pên-Tsao Ching* was apparently compiled about the 2nd Century A.D. (Chou, 1957, 1980; Konishi & Itô, 1973). Scarabaeoid beetles and mole crickets were among the soil-inhabiting fauna mentioned.

THE EARLY AND MIDDLE MEDIAEVAL PERIODS

By the second half of the 5th Century A.D., with the rise of barbarism and the demise of "classical" traditions, European culture was sinking to its lowest ebb. Give or take a century or so, this was also true, to a greater or lesser degree, of most other civilizations including that of China (and possibly also in the Americas). In about 500 A.D., however, another edition of the Chinese *Shen-nung Pên-Tsao Ching* pharmacopoeia by T'ao Hung-Ching was produced (Konishi & Itô, 1973), though it does not seem to have added much actual information to the 2nd Century version already noted.

For long after the decline of the Western Roman Empire there was no science in Europe, though some semblance of culture and scholarship eked out a rather precarious existence in Ireland (devoid of Greek) and in the Eastern (Byzantine) Empire. In zoology, apart from some transcriptions of old Hellenic works in the latter region (cf. Kádár, 1978), only the *Physiologus* persisted, but even that was placed on the list of proscribed and heretical writings by the Roman Church in 496 A.D. The ban was not lifted for just over a century. The earliest Mediaeval Latin versions of the *Physiologus*, judging by the oldest surviving copies now available (8th and 9th Centuries) varied little in substance, accounting for some 43 animals (mainly mammals and birds, as noted by George, 1981) in 48 or 49 chapters (see also James, 1928; T.M. White, 1954; McCulloch, 1962). There was thus a slight reduction from the "late classical" 56 animals already mentioned for the Greek text by Bodenheimer (1928) and Morge (1973). The Latin versions, for example, did not refer to scarab beetles. Among soil inhabitants, these insects symbolized heresy and their dung-balls evil thoughts; and ants were symbols of provident virtue (encouragement of the "work ethic" - which some to-day might also regard as heresy! - among the peasantry being important politically to both religious and secular institutions). Ants were also noted for their wisdom, particularly, in the present context, for their astuteness in biting grains in two to prevent their germination when stored in the soil.



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Fig. 12. "Ant-lions" or "ant-dogs" (see text, p. 383) from an early 14th-Century Anglo-Latin "Bestiary," in the British Library, London (MS Royal, 2B, VII, fol. 96; cf. George, 1981).

(That ants do neither this, nor reject barley in preference to wheat, was immaterial). The "ant-lion" (or "ant-dog"), derived from the gold-digging ants of the ancients (cf. George, 1981), was hybrid - yes, between lion and ant! - that symbolized man's ambivalence: its carnivorous front part, dominated by its vegetarian rear part, and *vice versa*, meant that it could eat neither meat nor plant material and so, though paradoxically surviving, it perished due to starvation soon after birth! Unlike its later namesake it did not live in pits in sand or soil. At least one Mediaeval illustration later showed it as a dog-like mammal inhabiting mounds of earth (Fig. 12).

By the 7th Century, the great plague of the mid 6th Century in the Mediterranean region had come and gone, and the worst was over - "culturewise" at least - in both Occident and Orient. It was early in that century that the glimmerings of biological science began to revive when Isidoro de Sevilla (Isidorus Hispaniensis) produced his encyclopaedic *Origines sive Etymologiae*. This not only borrowed from, but was later to contribute additional material to, the *Physiologus*, resulting in the development of the second "family" of *Libri Bestiarum* or "Bestiaries". Amongst the animals considered by Isidoro were the amphisbaena, the mole, and a handful of invertebrates, including earthworms and one or two soil-dwelling beetles (Bodenheimer, 1928, 1929; Morge, 1973). Isidoro's "cicadas", however, were Cercopidae (originating in the saliva of cuckoos, not in the soil like true cicadas). In passing we might also mention, in the 7th Century, Aldhelm (639-709 A.D.), England's first great scholar and senior contemporary of Northumbria's Baeda or "Venerable Bede". When prior of Malmesbury, Aldhelm composed, in Latin verse around 695 A.D.,⁸ his famous 100 "Riddles" (*Aenigmata Aldhelmi*) as part of his *Epistola ad Acircium* (Letter to Aldfrith [King of Northumbria]; see

Pitman, 1925). The reason for referring to Aldhelm here is not that he really mentioned the soil fauna, but to draw attention to a general omission in histories of biology. Aldhelm, though not prolific in the field, was one of the few first-hand recorders of nature during the millennium since Aristotēles. His only riddle remotely associated with soil fauna uncharacteristically concerned the "*Myrmicoleon*" or "ant-lion" in the mythical, symbolic tradition of the *Physiologus*.⁹ Baeda (Bede, 673–735 A.D.) in his *Natura Rerum*, of about 725, did not, so far as I know, refer to the soil fauna at all.

Also, in passing, we might mention the anonymous Old English epic poem. *The Deeds of Beowulf*, probably the oldest surviving major poem in a western "modern" language. This deals, in part, with events of the early 6th Century, but was apparently composed in the late 7th, or more likely early 8th Century (the only known manuscript is late 10th Century). Beowulf, the mighty hero, was eventually wounded by a gigantic, fire-breathing, subterranean Wurm or Worm (alternatively, Dragon - see Earle, 1892), which may be equated with The Mediaeval "*Daemon subterraneum truculentus*" (see footnote to Table I).

In the first part of the 9th Century, the German bishop Rhabanus Maurus completed his *De Universo*, which, though it drew heavily on Isidoro de Sevilla, was a much more erudite work than his. In it (Bodenheimer, 1928; Morge, 1973) he mentioned "*vermes*" of various sorts (including anything from fleas to clothes-moth larvae), some of which may have been true (annelid) earthworms or possibly terrestrial beetle larvae. He also referred to "*scarabaeus*" beetles (*Geotrupes*), to (field) crickets (*Gryllus*, *s. str.*, which burrow backwards into the soil and which are hunted by ants wielding hairs - a distortion from Nigidius, see p. 382), and to ants, with their various virtues. These last also included the fearsome, Indian giant gold-diggers of the ancients, formerly confused with "ant-lions", and transferred by him to "Aethiopia" (in accordance with Solinus, *antea*, and Isidoro). For apparently the first time, too, a *true* insect ant-lion (*Myrmeleon*)¹⁰ was mentioned, under the latinized name of *formicaleon* (perhaps to distinguish it from the mythical *myrmecoleon*). It is described as a veritable lion amongst ants, burrowing in the dust and killing its victims as they carry along their loads. His "*cicadae*", however, like those of Isidoro, were Cercopidae and their nymphs not soil-dwelling.

By contrast, in the early 9th Century (and probably long before), the development of cicadas (*ts'ān*) from eggs laid in the soil was widely known in China, as exemplified by a poem by Po Chu-I, quoted by Kevan (1983a: 42–43). Kevan (*op. cit.*) also quotes other Chinese and Sanskrit poems of the period (late 8th to 9th Centuries) that refer to cicadas, mole crickets, termites and/or ants, though few are pedologically oriented.

A notable western scholar of the middle 9th Century was the Irishman, John (the) Scot (Johannes Scotus Erigena, *ca.* 810 - *ca.* 877; the Scots, *sensu stricto*, originally came from Ireland!). His *De Divisione Naturale*, written between 865 and 870, included much original thinking - presumably contributing to its subsequent condemnation by the Roman Church - but, as it drew mainly on "Pseudo-Dyonisius" and similar authors of antiquity, it again gives us nothing to note on soil fauna. The 9th Century was also notable for the rise of Saracen¹¹ scholarship. Early in this period, there were translations into Syriac and Arabic of old Hellenic writings, including those of Aristotēles, now lost in the original. In the middle of the century, however, at about the time that John Scot was most active, an independent zoological work, the *Kitabal-Ḥayawan* (*Books on Animals*), was compiled by Al-Gahiz (or Aljahid). Regrettably it too, included virtually nothing on soil animals, other than some generalities on beetles in Book 3, and on ants in Book 4 (Bodenheimer, 1928). The later, better-known author, Ibn-Sina ("Avicenna"), of the late 10th to early 11th Century, was, it seems, merely a translator, whose

most valuable contribution was to be among those who helped to preserve the writings of Aristotēles. He did, however, discuss the amphisbaena, whose Arabic name was given as *auksimem*. During the 10th Century, too, other old Hellenic texts were being transcribed under the influence of the Byzantine rulers of Constantinople (Kádár, 1978), but nothing original transpired. Thus it was that, by 1000 A.D., soil zoology, like most other scientific disciplines, had progressed little further than these early works - where they had not, in fact, retrogressed.

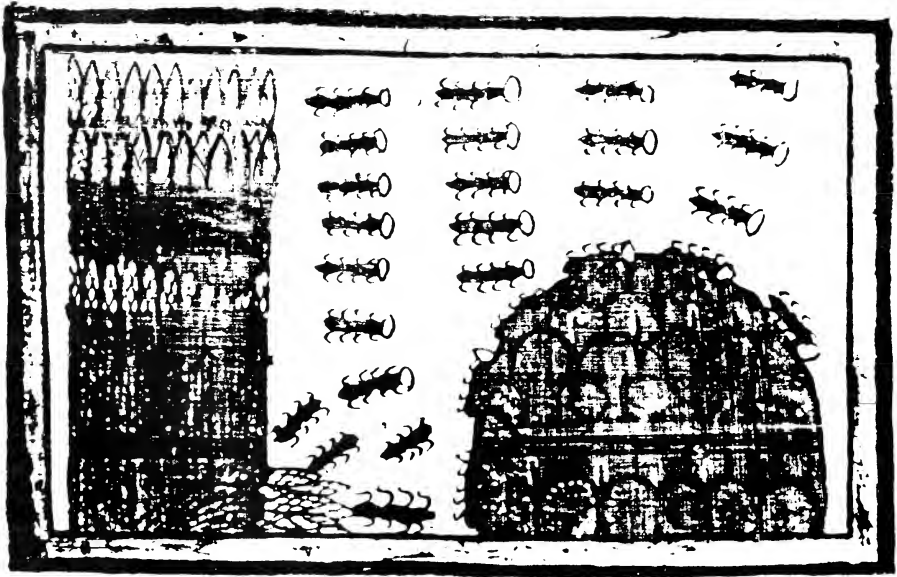
The 11th and 12th Centuries, pedobiologically, were no more fertile, though imagination and moralizing (e.g., in respect of ants) increased slightly in the shrunken *Physiologus* (see, for example, James, 1928; Rendell, 1928; McCulloch, 1962) and the appearance in church architecture of relatively uncomplicated forms of the amphisbaena (Druce, 1910). We may, however, mention a few works marginally associated with soil fauna, though the late 11th-Century comments by Shlomo Jizechaki (or Rashi), on insects mentioned in the Talmud, cited by Morge (1973), do not seem relevant. In China, there was a revived interest in pharmacopoeias and the old *pên-tsao's* were restructured along taxonomic lines in the form of the *Chêng-Lei Pên-tsao (Reorganized Pharmacopoeia)* by T'ang Shen-Wein in 1108 (Konishi & Itô, 1973). This discussed, amongst vermin and other lowly creatures, scarabaeoid beetles and mole crickets (Bodenheimer, 1928, 1929). Not long afterwards, in Germany, the Benedictine abbess, Hildegard ("St. Hildegardis")¹² began compiling her *Libris Physicis*, which may be said to date from about the middle of the century. Her work differed from earlier "herbals" as it was based on personal experience and local usage, not upon established "authority" and hearsay. Field crickets (which she called "cicadae") had certain medicinal properties; and she also mentioned ants.

Another mid-12th Century author, of great erudition (according to himself) and extreme verbosity, was Iōánnēs Tzétzēs of Constantinople, whose enormous metrical (one cannot say poetical!) work, *Biblos Histōrikē* (commonly called *Chilediades*), written about 1165-1170, included a fair amount of animal lore among his (un)natural history verses. However, he said nothing not already written by earlier authors. Examples of his writings (on cicadas, though not in soil) are given by Kevan (1983a). The mid 12th Century also produced the work of the Saracen scholar Ibn-Rashid (or "Averroes"), another major translator of Aristotēles, but not, a contributor. In this period, too, we should mention the credulous Anglo-Latin work of the Englishman Alexander Neckam, *De Naturis Rerum*, of 1170 (cf. Wright, 1863a; Raven, 1947), and of the even more credulous Norman-Welsh Silvester Gerald de Barri, or Giraldus Cambrensis, *Topographia Hibernicae*, of 1182 (cf. Wright, 1863b; Raven, 1947), if only in a negative sense. Though both works refer quite extensively to natural (and unnatural) history, including mention of insects, spiders and other invertebrates, the former refers, among soil-dwellers, only to the mythical amphisb(a)ena and the "seps" (probably based on a gecko, but which could mean almost anything from a poisonous serpent-lizard to a woodlouse or a myriapod), and the latter to the badger which is said to dig burrows in the earth.

The late 12th Century was the time when "Bestiaries" (*Libri Bestiarum*) not only started to become more elaborate, but when the numbers and complexity of "species" (real as well as "derived") mentioned therein increased (cf. James, 1928; T.M. White, 1954; McCulloch, 1962). In the early 12th Century, they had typically included relatively few (about 36) chapters, like the Latin *Physiologus*. By some curious turn of events (most likely due to inadvertent omission of a passage by some copyist, though I have not seen this theory advanced), the "*mermecolion*" later generally became confused with the *margarita*, or pearl, as was the case in the 12th-Century manuscript discussed by James (1928) and T.M. White



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Fig. 13. "Millipede" (resembling *Glomeris*; possibly an isopod crustacean *Armadillidium*) from 13th/14th-Century manuscript in the British Library, London (MS Harley 3244), apparently copied from an earlier (12th Century) Latin "Bestiary" (probably English). In the present manuscript, above this illustration is one of "vermes" ("life history" of earthworm) and another of spiders (with 7 pairs of legs!); below are mouse-like (or more probably shrew-like) "scorpions" (named in bottom line of text as shown); most of the above will be found (in white on black) in Davis (1958). Fig. 14. Industrious (8-legged!) ants carrying "grain" (pupal cocoons). From a Mediaeval "Bestiary" of (?) 13th Century (Pierpoint Morgan Library, New York, MS. 81, f. 311 - cf. Rowland, 1973).

(1954). Thereafter it tended to disappear altogether. The manuscript mentioned above included some chapters relevant to the present context: on mole, ant, "*amphivena*" (amphisbaena, but winged and no longer soil-inhabiting - cf. Fig. 7, 8) and "*vermis*". The last included earthworms, but also (in the tradition of Isidoro and Rhabanus Maurus) a wide range of arthropods, amongst which were scorpions, spiders, "millipedes" that rolled up into a ball (i.e., either *Glomeris* diplopods or *Armadillidium* isopods - cf. Fig. 13) and "termites" (by which seemed to be understood, almost any kind of wood-feeding insect *other* than true termites!).

In China, during this period, versions of the *Erh-ya* encyclopaedia and the *pên-tsao* pharmacopoeias with their occasional references to soil fauna continued to appear.

THE LATER MEDIAEVAL PERIOD

We may continue the story in China with a single reference of marginal pedobiological interest. Ever since the later T'ang-dynasty period (8th Century), crickets had been admired and kept for their songs, but, by later centuries, cricket fighting had become an important part of Chinese culture. As large wagers were made on the outcomes of the encounters, much care was lavished on the contestants. This demanded a basic knowledge of cricket biology (particularly as regards their care and maintenance). As fighting crickets are all ground-dwelling species, a number of which burrow in soil, a fair amount was known of such species. An extensive manual on the subject was written by a member of the Sung-dynasty court, Kia Sê-Tao, at the beginning of the 13th Century. It was called *Tsu-chi King*, or *The Cricket Book* (see Chou, 1957, 1980; Petit & Théodoridès, 1962). Needless to say there were successors in Ming-dynasty and later times.

With reference to crickets, it is also interesting to note that these were mentioned in the longer, 71-chapter, version of *Bestiaire* written in northern France before 1218 by one Pierre (called "le Picard" or "de Beauvais"). The insects were called *cri(s)non* or *gresillon* and were said to sing so much that they lose their appetites, forget everything else, let themselves be hunted and die singing. (This is really a distorted cicada myth.) One 13th Century manuscript of this work illustrates the cricket in front of a hole in the soil, though a 14th-Century one shows crickets on a hearth (McCulloch, 1962).¹³

In 13th-Century Christian Europe, though the "Bestiaries" (Fig. 14) remained the main sources of zoological (mis)information, scholarship began slowly to emerge from the stagnant morass into which it had sunk. To some extent this resulted from, and in others it paralleled, the Saracen advances in knowledge and the rereading of classical authors. Three major encyclopaedias compiled by members of the Christian Dominican order, and one by a Franciscan, all written between 1230 and 1270, referred to a few members of the soil fauna. The works are briefly reviewed by Bodenheimer (1928, 1929) and, through him, by Morge (1973). They are those of Thomas de Cantimpré, or Catimpratornus (*Liber de Naturis Rerum*, 1233-1248), of his apparent mentor, Albert von Bollstädt, or Albertus Magnus (*De Animalibus*, in his *Opus Naturarum*), 1255-1270, of Vincent de Beauvais, or Vincentius Bellovacensis (*Speculum Maius Tripartitum [naturale, historiale et doctrinale]*, the relevant parts, I, Books 17-23, also ca. mid 13th Century), and of Bartholomew (Glanville? the English, or Bartolomeus Anglicus (*De Proprietatibus Rerum*, of roughly the same date - see Raven, 1947). These authors, between them, mentioned moles, earthworms, amphisbaenas, ants (including their larvae and pupae), true ant-lions, crickets (often confused with cicadas), various beetles (including ground-beetles) and their larvae, and so on, but, apart from Albertus'

دانا الراحدا الله تعالى الرب وتطلى البواشيز تذهب به واذا كثر خنثا بصغير واخذت الميل
 وعينه به واكتحل برطوبتها شيع من الرمد وبها شريفا
 وتغلى بشي من الادهان وتغطى به الاهدق بزل الطرش والبغير
 اذا البلع الحنثا في وسط عليه يرون ترخدا الحنثا وفي وسط
 الروث في كثره جيا واذا طرحت خنثا على غرابان الغراب
 رثها صنف نبال له الجبل دورا الزل وشي يدل ايها اذا تركها في وسط الورث شك خنثي منها مائة وبعد

15



16

Opimacus
 Opimacus vermis corpore exiguus sed animo
 clarus. dicitur enim cum serpentibus habere
 certamen et plerumq; ingenio eos superare pu-
 gne exeruit

17



Fig. 15. Scarabaeoid beetles (*khunfusa*) from the Arabic manuscript (Munich Codex) of H. Al-Qazwini's *Nuzhat-ul-Qulub*, originally written in 1341. After Bodenheimer (1928), who says that the illustration probably originated during the lifetime of the author, and perhaps under his supervision. Fig. 16. The Bishop of Lausanne excommunicating cockchafers in the 15th Century. Copied from a contemporary illustration, after Bodenheimer (1928). Fig. 17. Mole-cricket, *Opimacus*, now *Gryllotalpa*; water-colour from Book IV of the *Codex Animalium* of Petrus Candidus Decembrius, ca. 1460. After Bodenheimer (1928).

denial that the amphisbaena had two heads, they still really had nothing to say on these animals that had not been said previously, mostly by the *Physiologus* and by Aristotēles.¹⁴ In the very early 1300's (1304–1309), Pietro de Crescenzi (Petrus Crescentii), in his *Ruralium Commodorum Libri XII*, dealt with crop pests, though mostly on the basis of reports by classical authors. Once more, soil-inhabiting forms do not appear to have been considered, though he did recommend certain remedial measures for the control of ants (Bodenheimer, 1928; Morge, 1973).

Meanwhile, the Saracen scholars were gradually expanding knowledge in many fields (though scarcely in relation to soil fauna). The cosmography of Zakariyā bin-Mohammad bin-Maḥmūd Al-Kummūnī Al-Qazwīnī (cf. Wiedemann, 1916; Bodenheimer, 1928), the 'Ajā'kh al-Makhlūqāt (*Wonders of Creation*), completed in 1263, refers briefly to earthworms, ants, scarabaeoid beetles and crickets. This work was drawn upon and expanded by another Al-Qazwīnī (Ḥamdullāh Al-Mustaufā of that ilk) in his encyclopaedia, *Nuzhat-ul-Qulūb* (*Hearts' Delight*), of 1341 (cf. Stephenson, 1928). Soil animals mentioned included termites (*araḍat*; they eat earth and are attacked by ants), woodlice (*ḥimāru-l-qabban*), earthworms (*kharāṭin*; with medicinal and aphrodisiac properties), beetles (*khunfusa*; including small scarabaeoids, Fig. 15), various "worms" (*dūd*; including insect larvae of divers kinds, some subterranean), crickets (*ṣarṣari* in Persian; *tātūk* in Arabic; with medicinal properties) and ants (*naml*; various kinds enumerated).

A little prior to this work, in 1320, we have what is probably the first involvement of the Christian Church in the control of soil pests - though against the aerial adults - the excommunication of May-beetles (*Melolontha*) at Avignon. Similar exercises in exorcism (Fig. 16) continued for centuries, since pest outbreaks always diminished thereafter - eventually!

One of the landmarks of Mediaeval biological literature was undoubtedly the great zoological lexicon, the *Ḥayāt al-Ḥayawān* (*Life of Animals*), completed in the late 14th Century, by the Egyptian scholar Kamal Ad-Din Ad-Damīrī (see Jayakar, 1906, 1908; Bodenheimer, 1928, 1929; Morge, 1973). Soil-inhabiting animals were mostly of the same kinds, with much the same information, as included by the Al-Qazwīnī's: Termites (*al-'arada, as-surfāh*), various insect larvae (*al-asāri*), including some subterranean, field crickets (*al-gudgud, sharrār al-lail*), scarab beetles (*al-gu'āl*; dung-feeding by larvae noted); "worms" (*ad-dūd*; including earthworms and a range of insect larvae, but also termites and [parasitic] nematodes), a "worm" that rolls up in a ball (*ash-sha'hamat al ard*; either an *Armadillidium*-like isopod or a *Glomeris*-like millipede), woodlice (*himār-kabbān*), earwigs (*al-'ukubān*) and dung beetles (*qish'ibān*), as well as a whole range of ants (*naml*, generally; *al-gathlah*, black; *ad-dinnah*; *ad-dharr*, small, red; *as-simsimah*; *ash-shaisabān*, male; *at-thathrag*; *al-'ugrūf*, ? carpenter; *'aygabuf*; *hayzabūn*; *al-fazir*; *mūq*, winged; and *heigemāna*, very small). Although Ad-Damīrī was comprehensive, he was not particularly innovative or informative, especially in terms of soil-fauna relationships.

In these times, also, other writers of the Islamic world mention something of various agricultural insect pests, but, to all intents and purposes, relating only to those above ground. Several of the zoological and agricultural works, and copies later made from them, included illustrations of the animals. These were, however, seldom, if ever, drawn from nature - locusts were often bipedal and like birds, and (almost in the present context) crickets quadrupedal and like newts!

When considering the 14th Century, one should perhaps not be surprised at the lack of progress for, in the very middle of it, came the Black Death. This was by no means confined to

Europe, but it was most terrible there, especially from 1347 until 1350. This plague (followed by severe typhus epidemics) had dreadful and lasting consequences for human activities of all kinds, including scholarship. At least a quarter, and probably a third of the entire population of Europe died. Like Ad-Damīrī in Cairo, Cunrat von Megenberg, who translated Thomas de Cantimpré's *De Naturis Rerum* into German (*Das Püch [= Buch] der Natur*) about this time (see Note 14), survived in Regensburg, but many scholars did not. Then, a century later, came another major catastrophe for Christendom (though less so for scholarship); the Byzantine Empire fell to the Osmanli Turks in 1453.

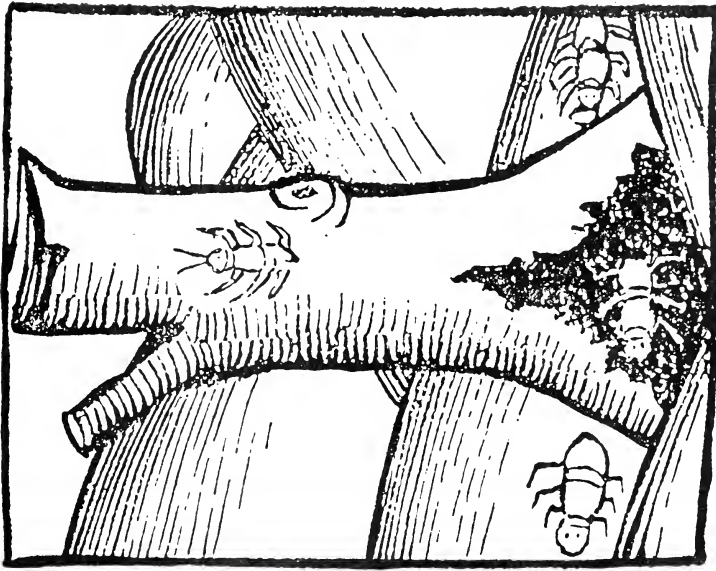
Scholastic recovery from this second disaster was not so slow as from the Black Death, for the Renaissance, spurred on by the resulting economic revolution in its wake, was already beginning. The Middle Ages had come and gone, and within less than half a century, both in the Far East (where it had long been known) and in the West, the era of the almost *universal* use of printing had arrived.

Belonging to the scientifically rather sterile transitional period of the early Renaissance, but Mediaeval in tradition, we may note in passing the beautifully illustrated *Codex Animalium* of Petrus Candidus Decembrus, about 1460 (*cf.* Bodenheimer, 1928, 1929; Morge, 1973). This drew heavily on the 13th-Century European encyclopaedias (and on old Plinius Secundus!). It contributed nothing new, but, in its fourth volume, it included references to various "worms" and insects, such as ants and "cicadas" (really crickets), and excellent watercolours of a mole cricket (called *Opimacus*, Fig. 17), and of a true (if 4-legged) ant-lion larva (see Bodenheimer, 1928). Here, too, it would seem appropriate to place what would appear to be the first definite evidence since the ancient Sumerians of discrimination between species of earthworms. *A Treatyse of Fysshynge wyth an Angle*, attributed (possibly erroneously) to Dame Julyana Barnes (born ? *ca.* 1388), Prioress of Sopwell Nunnery, Hertfordshire, England, recommends the "great angle Twytch" (probably *Lumbricus terrestris* or *Allolobophora longa* or both) for catching eels, but "red" worms for all other fish. A manuscript (perhaps of as late as 1479, and thus presumably posthumous to the alleged authoress) exists (T. Satchell, 1883); printed versions also exist, that under the name of Julyana Berners (1496) being the earliest.¹⁵

THE RENAISSANCE

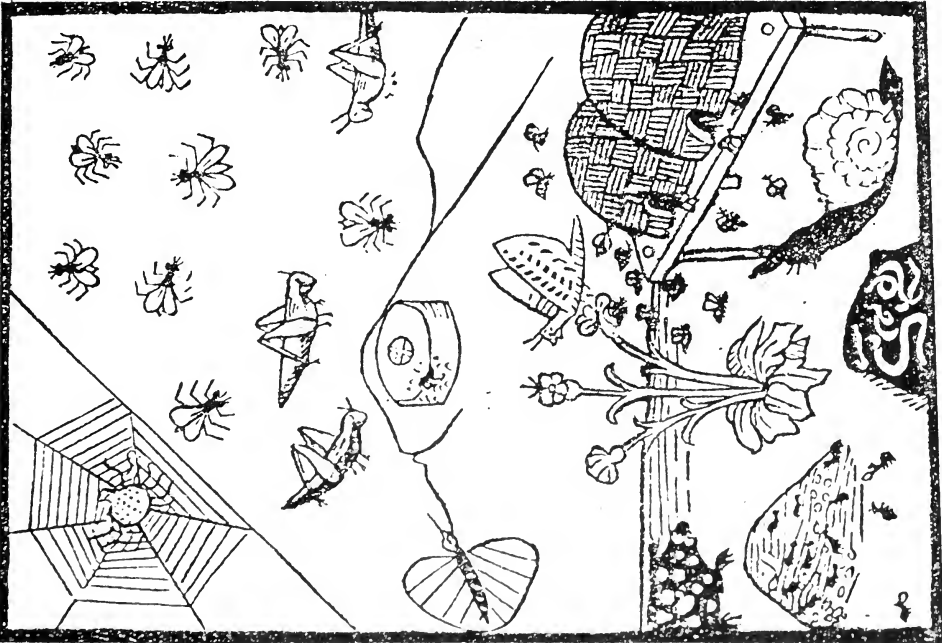
The European Renaissance was no sudden phenomenon, and it developed at different times in different places, but we can think of it as occupying much of the 15th through to the middle of the 17th Centuries. In the Orient, also, there were roughly coincident changes in Chinese philosophy, but these were not so marked nor did they so radically affect attitudes toward learning in general and science in particular. The European entomological and associated literature of this period is briefly reviewed by Beier (1973), though he makes virtually no reference to soil fauna. Some scattered information on the topic is, however, "buried" in Bodenheimer's "History of Entomology" (1928, 1929).

Immediately after the widespread adoption of printing, already mentioned, there was less immediate change in biological knowledge than might be anticipated, and the old works prevailed in printed, rather than manuscript form. Bartholomaeus Anglicus' mid-13th-Century *De Proprietatibus Rerum* appeared in a first printed edition in 1470, and Cunrat von Megenburg's mid-14th-Century *Das Püch [= Buch] der Natur* in 1475, became the first illustrated, printed natural history book (see above and Fig. 18). Not long afterwards appeared (*Fysshynge wyth an Angle*, see above) and the first edition (of many) of *Ortus* (or *Hortus*)



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Fig. 18. Folding woodblock "plate" including ants and earthworms, from Cunrat von Megenberg's (1475) *Das Puch der Natur* from Mss. of the middle of the previous century. Fig. 19. Ants emerging from the ground, illustrating the section "Formica" in an early printed version of *Ortus Sanitatis* (see p. 390), ca. 1500. After Bodenheimer (1928).



18



20

Fig. 20. Mushrooms, earthworms, snail, etc., 16th Century. Above, woodcut from Lyons (French) edition, 1572, of Mattioli's (1548) *Commentario*. Below, embroidery (34x34cm) based on the same, by (or under the direction of) Elizabeth, Lady Shrewsbury ("Bess of Hardwick"), ca. 1580; one of a series now at Hardwick Hall, Derbyshire, England; note prominent isopods above the earthworm. [From a photograph.]

7

GEORGII AGRICOLAE DE ANIMANTIBVS
subterraneis Liber.



CORPVS subterraneum, ut res ipsa demonstrat, in animatum distribuitur, & inanimatum. quod autem animi expers est, rursus diuiditur in id quod sua sponte erumpit ex terra, & in id quod ex eadem effoditur. De altero inanimati genere dixi in quatuor libris de natura eorum quæ effluunt ex terra inscriptis, de altero in decem de natura fossilium: nunc de subterraneis animantibus dicam. Cum uerò genus animantium omne constet ex quatuor elementis, & corpus humidum ac siccum, id est aqua & terra, ad accipiendum apta sint, necesse est ea ipsa duo elementa animantium materiam esse. Ex quo rursus illud quadam naturæ necessitate consequitur, ut omne animal & in aqua uel terra gignatur, & in eis commoretur atque uita fruatur. Nam bestię uolucres,

a 4 etli

Sanitatis, a sort of herbal-cum-pharmacopoeia based upon the various Mediaeval encyclopaedias already mentioned. It has been attributed to Johann Wonnecke (or Dronnecke) van C'aub (Johannes de Cube or John Cuba), though some consider him to have been merely the translator of the work into German (*cf.* Wonnecke van C'aub, 1480, 1485). Jacobus Meydenbach (1491) has also been credited with the authorship, though he was but the editor of a somewhat later, better known, edition. Bodenheimer (1928, 1929) briefly reviews the latter and later editions from an entomological viewpoint. (Insects were not mentioned in the smaller, earlier edition). Soil-dwelling insects mentioned included ants (Fig. 19), true cicadas (as well as Cercopidae), scarabaeoid beetles and field crickets. The *Hortus Sanitatis* spawned various other herbals in the 16th Century, but, like the "Bestiaries" that were still popular, these contributed nothing to the advancement of science, pedobiological or otherwise. In the "Bestiaries" the religious and moral emphasis became, if anything, even greater and led to the publication of works virtually devoid of interest in biology, such as the *Reductoria Moralia* of Petrus Berchovius, 1521 (see Bodenheimer, 1928, 1929). Soil-inhabiting animals mentioned therein included the same old range of ants, "ant-lions," cicadas, crickets (deadly poisonous insects!) and so forth.¹⁶ The *Hortus Sanitatis* also encouraged more practical books like the *Commentario* of Pietro Andrea Mattioli or Matthiolus (1548) and the *Naturalis Historiae* of Adam(us) Lonicer(us) (1551). The former, at least in some later editions, includes an illustration showing earthworms (Fig. 20) and support for the view that the amphisbaena has only one head, though reference to other soil fauna is virtually lacking. The latter work (see also Bodenheimer, 1928) mentions ants and scarabaeoid beetles (notably the Rose Chafer, *Cetonia*), crickets, "earth flies" and "earth fleas". It would be pleasing to think that the last constituted the earliest specific reference to Collembola (among the most characteristic of all the soil fauna), but, alas, flea-beetles are more probable, for control of garden pests was being discussed.

Between the dates of publication of these two works (which maintain a Mediaeval quality) came the first ever that we can really relate specifically to the soil fauna, though even this was marginal and dealt very largely with vertebrates. This was *De Animantibus Subterraneis* (Fig. 21), published in Basel by Georg Bauer under the alias of Georgius Agricola (1549).¹⁷ Although generally descriptive of the fauna, the book emphasizes animals that dig or tunnel in the ground, some of which (such as rabbits and foxes) present-day soil zoologists scarcely consider as constituting part of the true subterranean fauna. Little in respect of the latter is actually discussed. The book was innovative in that it adopted an interdisciplinary, ecological approach, though to-day most would probably consider it (even though it be in Latin!) to be largely "waffle" (a feature by no means alien to many ecological writings!)

Agricola (*op. cit.*) divided his "subterranean" fauna into two main categories, "permanent" and "occasional," but this division did not apply to the entire life-cycles of the animals considered. For example, ants, wasps (*Vespula*), hornets (*Vespa*) and crickets, as well as scarabaeoid larvae, were all considered to belong to the category whose association with the underground was "permanent", whilst such insects as bees and cockroaches were but "occasional". Table I indicates those animals mentioned by him that (with the exception of *Blattae* and "*Gryllus domesticus*") we might consider to have rather more than a merely temporary association with the soil or litter. Woodlice ("*Asellus*") were, however, only mentioned as hiding in cracks in walls and in houses ("*rimis parietum & domorum latebris occultantur*"). The "*scolopendrae*" (centipedes and/or millipedes) were said to be found in [fallen] tree-trunks or in wood placed upon the ground or in sticks loose in the earth

TABLE I

Alphabetical list of German Subterranean Animals that can Conceivably be Classed as Soil Fauna, as Categorized by Georg Bauer (Agricola, 1549)

Category*	"Classical" name used	Old Alsatian German name used	Modern High German equivalent	English equivalent	Current scientific name
Gradientium (Of Walkers)	<i>Asellus</i> †	<i>schefflein</i>	<i>Schäfflein</i>	"lambkin," i.e. woodlouse, sowbug	Isopoda,
	<i>Blattae</i> †	Wiebel, <i>brotworme</i> †, <i>spring wiebel</i>	Wiebel, <i>s.l.</i> = Käfer, Brotwurm	"weevils"; cock- roaches; etc.	Oniscoidea Coleoptera; Blattodea
	<i>Formica</i>	<i>eims</i>	<i>Schabe, s.l.</i>		
	<i>Scarabaeus</i>	[here] <i>sewkefer</i>	<i>Ameise</i>	ant, emmet	Formicidae
	<i>Sorex</i>	<i>spitzmaus, feltmaus</i>	<i>Seufkäfer</i>	dor-beetle	<i>Geotrupes et al.</i>
	<i>Talpa</i>	<i>molwurff</i>	<i>Spitzmaus</i>	shrew(mouse)	<i>Sorex</i>
	<i>Vermis in Maio netus</i>	<i>meiworm</i> §	<i>Maulwurf</i>	mole	<i>Talpa</i>
			<i>Maikäferlarve</i> , Egerling	May-beetle larva, Cockchafer larva,	<i>Melolontha et al.</i>
	<i>Vormela</i>	<i>Wormlein</i>	<i>Würmlein</i> ,	Whitegrub	
			<i>Würmchen</i>	small "worms", grubs	Insecta (larvae)
Volantium (Of Flyers)	<i>Gryllus domesticus</i>	<i>hausheim</i>	<i>Heimchen</i>	House cricket	<i>Acheta domesticus</i>
	<i>Gryllus agrestis</i>	<i>feldheim</i>	<i>Feldgrille</i>	Field cricket	<i>Gryllus campestris</i>
Serpentium (Of Serpents)	Amphisbaena, Ignota	[unbekannt]	Amphisbāna	Amphisbena	[mythical - see p. 375]
	Τυφλωστ, Τυφλωψ	<i>blindschleiche</i>	<i>Blindschleiche</i>	Slow-worm,	<i>Anguis fragilis</i>

(continued on next page)

TABLE I (continued)

Category*	"Classical" name used	Old Alsatian German name used	Modern High German equivalent	English equivalent	Current scientific name
<i>Vermium</i> (Of Worms)	<i>Lumbricus</i>	reinworm	<i>Regenwurm</i>	Blindworm rainworm, dew-worm, earthworm	Lumbricidae
<i>Not on List</i> (but referred to in text)	Spongylis Aranei nigri <i>Scolopendra</i>	<i>engerle</i> — —	Engerling "schwarze" Spinnen Hundertfüßler, oder ? <i>Tausendfüßler</i>	whitegrub "black" (? = wolf) spider centipede, or ? millipede	Scarabaeoidea (larva) Lycosidae? Chilopoda, or ? Diplopoda

*Omits categories Natantium (Of Swimmers), which are irrelevant, and *Daemonum* (Of Demons), which includes only the entry "*Demon subterraneum truculentus*" (Malevolent subterranean demon) or (Malevolent subterranean demon) or "*bergteufel*" (mountain devil), or the less evil "*bergnenkel/kobel/gutiel*" (gnomes, goblins, fairies, etc.).

†Referred to only from buildings, and, except for "*Asellus*," not soil-associated.

‡cf. Swedish "*brödetäre*".

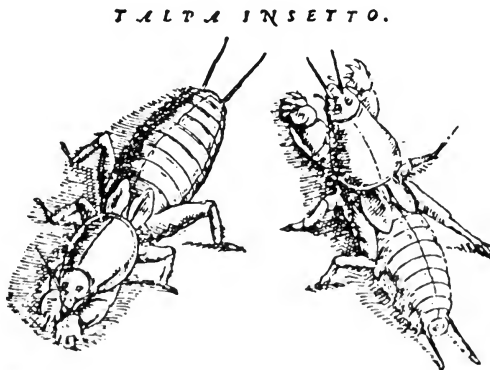
§Said to have only 4 legs.

("scolopendra in truncis arborum, aut in lignis supra terram locatis, aut in palis terrae infixis"). "Black" spiders ("*Aranei nigri*"), which I take to mean wolf spiders (Lycosidae), inhabit holes in the ground, as do field crickets ("*Gryllus agrestis*"). It was observed that the latter (and cockchafers or "*Vermis in Maio*") dig in dry earth in order to construct their burrows for the summer (House crickets for the winter also); field crickets die before winter; cockchafers in early autumn. It is also of interest to note that even in this scientifically-based work, credence is given to the existence of various subterranean demons. The (unknown) amphisbaena is also mentioned, presumably still in its dread, mythical Mediaeval form (see Note 6). Though Agricola's small book, as the first treatise on soil zoology, may be said to constitute something of a landmark in biological science, it had no impact on the study of soil animals, or of ecology generally, either at the time or subsequently. It has, in fact, rarely been cited.

De Differentiis Animalium, by the Oxford physician Edward Wotton (1552), should now be briefly mentioned for its refreshing style. It was, however, but a concise account of classical, zoological knowledge freed from the clutter of Mediaeval embellishment, and cannot be said to have contributed anything new. The soil-inhabiting animals were virtually the same as those mentioned by Aristotēles. Nigidius' account of the burrowing and capture of crickets (see p. 382) as well as a reiteration of their alleged medicinal properties, however, is given.

About the same time, the Swedish Archbishop Olaf Ster (Olaus Magnus Gothus) published his treatise on Scandinavia, including an account of its animals (Ster, 1555: Book XII). In complete contrast to Wotton, this was in the old, almost Mediaeval, tradition. Of soil-inhabiting animals, only ants were considered, though a fair range of their types of "nests" was covered. It was stated that a red (poisonous) species lived in mole-hills in meadows. Bodenheimer (1928), who refers to the above, also notes that Hieronymus Cardanus (Geronimo Cardano), in 1559, cited Albert von Bollstädt (see p. 387) on the question of true ant-lions, and stated that West Indian ants inflict painful bites.

Bodenheimer (1928) also mentioned the fact that Johann Colerus, in his "Household Book" of about 1500, referred to damage to plant roots by insects (for which remedies were prescribed), and he also draws upon the behaviour of ants in relation to weather prediction. Bodenheimer likewise draws attention to the local, but notably original observations of Dr.



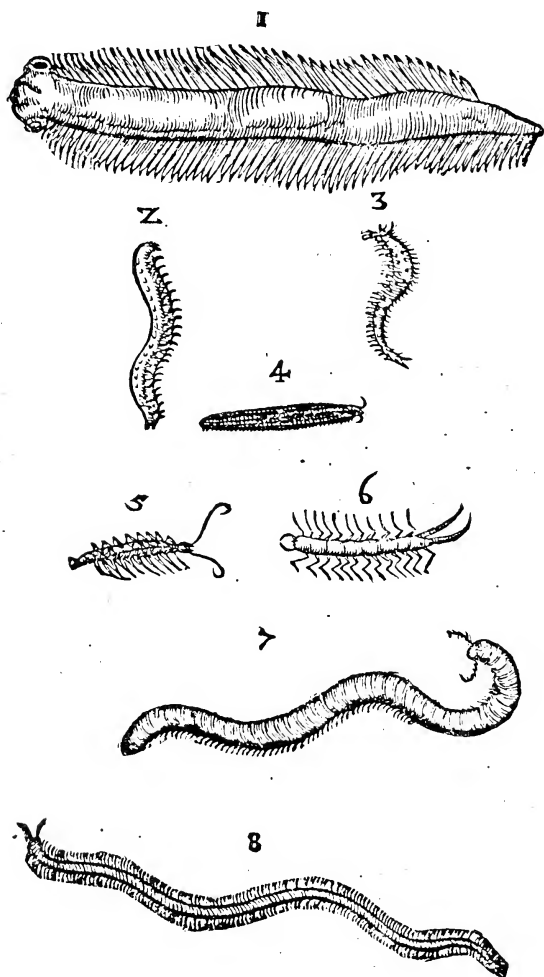
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Fig. 22. Mole-cricket, *Talpa Insetto* (now *Gryllotalpa*) from Ferrante Imperato (1599).

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Vlyssis Aldrouandi

Bicipitem verò esse Scolopendram verum non est, sed bicipitè poëta dixit, quòd talis videatur: nam vt Aristoteles testatur & experimento quotidie deprehendi potest, Scolopendra ex utraq; parte graditur, tanquã vtrinq; caput habeat vnum, etiam si in duas partes dissecta sit, tunc enim altera pars in caudam, altera mouetur in caput. Sed dum graditur, remorum instar, latos mouet pedes, quos alarum in modũ gestat, sicuti poëta dixit. ⁶ Theophrastus Scolopendras scribit reperiri circa radices gladioli, quia, inquit, congregantur facillimè in eam. Quibusdam in regionibus tanta copia increuere, vt fugati ab eis populi proprios deferuerint ¹ Li. 8. c. 29. lares, quod Trieriensibus contigisse scribit Theophrastus teste ¹ Plinio: idem de Rhytienibus prodidit & Ælianus. Quæ in hac tabula num. 1. depingitur Scolopendra est marina, lato corpore, subcastaneo, velut pedibus innumeris, longiusculis, aurei coloris. Num. 2. co-



23

Iore

Fig. 23. A page from *De Animalibus Insectis* by Ulysse Aldrovandi (1602), showing various forms of Scolopendrac (centipedes), including millipedes and marine polychaet worms (I). [Original in Lyman Collection, McGill University, Macdonald College Campus.]

Maxima terrestris Scolopendra, ea quam vides crassitie & longitudine est; color totius corporis ex fulco nigricante splendens. Singulis incisuris pedunculus appendet luteus, *id est*, in singulis lateribus sexaginta prorsum & retrorsum aqua facilitate promovet. Num et caput versus ingreditur, & in caudam; ideoque à Nicandro & Rhodigino biceps dicitur. Partem inter caput & alium non simplicem sed multiplicem habet: quo fit, ut præcisum hoc genus vivere possit. Irritatus hic Scolopendra tam acriter mordet, ut Ludovicus Atmarus (qui nobis eum à Libya dono dedit) quamvis chirothecis duplicique linteo munitus, vix eum manum petentem ferre poterit; altè enim in linteum os forcipatum adegerat, diuque pendulus vix tandem excuti permisit.



Horum alium ex nova Hispaniola allatum linea quædam flammea medium per dorsum ornat, atque æneus later pilorumque color commendat: habet enim capillares pedes, atque armatim se tollens celerrimè currit. Hoc summa admiratione dignum est, quum natura huic animalculo caput minimum dederit, memoriam tamen, vimque rationis æmulam, neque congio, nec urceo, sed amplissima quâdam mensura tribuisse: cum enim innumeri adsint pedes, quasi remiges, & à capite veluti clavo alij permultum distant; novit tamen quisque officium suum, & pro imperantis capitis mandato, in hanc vel illam partem se conferunt.



Alius item ad nos ab Augustini promontorio ex India perlatus, corpore nonnihil atque pedibus major, qui septuaginta livescentibus incisuris, & bis totidem spadiceis pedibus constabat.



Plures Scolopendras reperiri non dubito, omnium fere colorum, præter viridem: quamvis etiam Ardoynus de viridi mentionem facit. In sita singulis proprietas (ex Theophrasti sententiâ) ad Gladioli herbarum radices sese conferre. Bubulas autem exuvias meretur Robertus Constantinus, eumque secutus Stephanus, nec non Ardoynus ipse; qui Scolopendram primum serpentem, deinde octipedem, tum in cauda cornigerum, ultimo tardigradum esse comminiscuntur. Taxandi Rhodoginus, Alberus & Avicenna, quod nullum Insectum supra viginti pedes habere temerè affirmant, illique numero Scolopendram alligant. Quamvis etiam Nicandri biceps dicatur his versibus:

Johann Bauhin (1598) on "*Scarabaeus majalis*" (a geotrupid dor-beetle, illustrated), and what were clearly scarabaeoid larvae, made when graves were being dug near Mompelgard (Württemberg). About this time, too, (? 1593), the Neapolitan physician Ferrante Imperato (1599) included, in his book of natural history curiosities, a reasonably good illustrated account of the "*talpa insetto*" (i.e., the mole cricket, *Gryllotalpa*, Fig. 22). The closing years of the 16th Century also saw the invention, in 1590, of the microscope by the Dutchman Zacharias Jannsen, which, if one may be permitted to turn a phrase "opened up a whole new can of worms"¹⁸ for all of the biological sciences, and ultimately led to the discovery of the true nature and diversity of the soil fauna.

In China, the classical *pen-ts'ao* pharmacopoeia was restructured along biological rather than pharmacological lines, to produce the *Pên-ts'ao Kang-mu* of Lia Shih-Chên, completed in 1596 (Konishi and Itô, 1973). It referred to ants of three or four kinds, termites, burrowing (polyphagid) and other cockroaches, earwigs, mole crickets, field crickets, ant-lions and various kinds of beetles, such as Carabidae, Elateridae, Silphidae and Scarabaeoidea (including coprophagous species) and their larvae. Instructions were given on how to collect many of these insects. In the Orient, however, general knowledge of the soil-associated (and other) fauna had made virtually no advance since "Mediaeval" times and, indeed, never did so until caught up in the wake of 20th-Century western scientific advances.

The advent of the 17th Century may be said to have heralded a new era of invertebrate zoology, and of entomology (*sensu lato*) in particular. This has a direct bearing on the recognition of the more prominent members of the soil fauna. It did not, however, bring with it any real pedobiological advance.

The earliest two textbooks of entomology ever written both really belong to the 16th Century as they were too early to take advantage of the microscope. That of the wealthy Italian, Ulysse Aldrovandi (1602), *De Animalibus Insectis* (Fig. 23), has priority of publication, but the first to be "ready for press" (virtually completed 3.III.1589) was the *Insectorum Theatrum* (Fig. 24), compiled by Thomas Moffet, Moufet or Muffet, the London-born, much travelled physician of Scottish parentage who became a physician at the English court. The work itself, though not published until long after its compiler's death (Moufet, 1634), was known to some authors much earlier, and there may even have been an abortive, imperfect continental edition in 1598 (Raven, 1947). It combined Moffet's own observations with previously unpublished, posthumous manuscripts of Edward Wooton (above), the Swiss zoologist Conrad Gesner, and particularly of the illustrator and collaborator, another English physician, Thomas Penny (*not* Penn, as given by Bodenheimer, 1928, and Beier, 1973). The English translation (under the name of Muffet) did not appear until yet another quarter-century had passed, when it was combined in a single volume with reprints of the Reverend Edward Topsell's (1607, 1608) "Histories" of "Four-footed Beasts" and of "Serpents" (Topsell, 1658).

Both Aldrovandi and Moffet included invertebrates other than terrestrial arthropods. In the case of the latter author, these were restricted mainly to various kinds of worms, but the former dealt in addition with slugs and, quite extensively, with echinoderms. As much of Aldrovandi's tome, in contrast to the smaller volume of Moffet, was taken up with all manner of non-scientific (though often fascinating) material, the latter was, for the most part, scientifically the more satisfactory, though it, too, left much to be desired. Both dealt with a fairly wide range of soil- and litter-inhabiting animals, which, apart from the earthworms and slugs, are accounted for along with others by Bodenheimer (1928, 1929). Although the

publication of these works constituted a great stride forward for entomology, knowledge of the biology of the animals concerned was, nevertheless, advanced very little. Moffet (Mouffet, 1634), among soil-associated animals mentioned (and often figured) the following, in addition to earthworms: ants (which are categorized in an almost Mediaeval fashion), mole crickets (said to spend most of their lives in damp soil and to collect grains of wheat and oats, possibly for the winter), earwigs, various kinds of beetles (such as scarabaeoids, including their dung balls, ground-beetles, elaterids and staphylinids, as well as the subterranean larvae of some of these, such as wireworms and whitegrubs), field crickets and cicadas (whose soil-inhabiting nymphs were not emphasized). In addition to these insects there was mention of mites on geotrupid beetles (see also Oudemans, 1926) and of millepedes, centipedes, isopods and burrowing spiders, as well as scorpions. Aldrovandi (1602), besides discussing earthworms and slugs, covered much the same range of soil-associated arthropods as Moffet. He noted that chafers (*Melolontha*) dig "nests" in dry earth, assuming that, as with burrowing bees and digger wasps, they oviposit there. He also referred to and figured earth nests of Geotrupidae and mentioned root-feeding by whitegrubs and mole crickets. When writing on cicadas, he mentioned the amphisbaena in connection with Nikandros (see p. 376), but he dealt with it more fully, and illustrated it, in his posthumous, 1606, volume on reptiles and serpents, maintaining that the animal did indeed have two heads, contrary to the declarations of other authors (Druce, 1910).

In the same year that Aldrovandi (1602) published his *De Animalibus Insectis*, there appeared in Strassburg the anonymous *New Feld- und Ackerbau*, a revised and "modernized" version of Petrus de Crescenzi's *Ruralium Commodorum* of the early 14th Century (see p. 387), advising on how to deal with various pests, including "earth lice", whitegrubs and ants (Bodenheimer, 1928). In the following year, Schwenckfeld (1603), in the 6th book of his *Theriotropheum*, relating to the fauna of Silesia, dealt with insects in an alphabetical, but very comprehensive manner (cf. Bodenheimer, 1928). Soil-associated animals mentioned included the following: "*Ascarides terrenae*" (various insect larvae including whitegrubs, cutworms, and probably the maggots of bibionid Diptera, all of which damaged fields and cut off roots); "*Cantharis formicaria latior*" (*Cetonia aurata*, the Rose chafer, and its white-grub-like larva and pupa living commensally in ants' nests); "*Culices fematarii*" (various small, manure-inhabiting dipterous flies); "*Curtilla*" (mole cricket, *Gryllotalpa gryllotalpa*, a pest of roots which builds nests in the earth and lays yellowish eggs therein¹⁹); *Formica* (ants generally; life history given; the idea that ants become winged when older is perpetuated); *Fullo* (here meaning the Common earwig, *Forficula auricularia*, lives under tree-bark; the idea of propensity to creep into human ears perpetuated, and remedies given); *Gryllus agrestis* (= *G. campestris*, Field cricket; digs in dry earth and spends the summer underground in holes); *Scarabaeus pilularius* (= *Geotrupes stercorarius*, dor-beetle; makes big balls of dung, using its feet, and lays its little larvae therein to protect them from winter cold); *Scarabaeus bufonius* (= *Carabus auratus*, a large ground-beetle; lives where toads are plentiful; people believe that they copulate with these; they are likewise poisonous[!]); *Spondylis* (whitegrubs, *Melolontha* and similar larvae; garden pests which lie in the earth near plant roots which they completely devour; used by anglers as fish-bait).

We have already referred to the Reverend Edward Topsell in connection with the English translation of Moffet (see p. 400), but his *Historie of Serpents* (Topsell, 1608) should perhaps receive brief mention here. This work was based mainly on the work of Conrad Gesner (see p. 400), but, despite its title, includes some information on invertebrates, virtually all, with the

exception, so far as we are concerned here, of his notes on scorpions, taken from a pre-publication copy of Moffet. He does, however, mention a "discourse of Wormes" by his contemporary, Dr. Thomas Boreham. This does not now appear to be extant (Raven, 1947), which is a pity, as it would seem to have been the first treatise on earthworms as such, other than that attributed to Dame Juliana Barnes (see p. 390).

Before concluding this section, we should perhaps briefly mention Francis Bacon of Verulam (St. Albans), one of the most noted philosophers of his age, if only to note that, in his posthumous *Sylva Sylvarum* of 1627, he presented some observations and researches on insects (most of which he pronounced to be generated in filth) and earthworms. Despite his erudition, however, he had nothing to contribute to knowledge of the soil fauna (see Bodenheimer, 1928). Bodenheimer (*op. cit.*) also refers to the 1645 *Zootomia Democritaeta* of Marco Aurelio Severino, which includes some observations on the anatomy of crickets and (?) earwigs.

MID-17TH TO MID-18TH CENTURIES

Although Francis Bacon (above) had introduced new philosophical concepts, it was not until the 1640's that we see the beginnings of the "Rise of the Naturalists" (the "Bionomic Era" of Bodenheimer, 1928). Like other developments, this did not come about suddenly, but one particular name may be mentioned here, that of Dr. Thomas Browne (later Sir Thomas Brown - without an "e"!). This worthy English scholar began to raise biology to a scientific level by questioning "authority" - almost "for the first time since Aristotle", according to T.H. White (1954), though John Scot (see p. 384) apparently found himself in disfavour on a similar account several centuries previously. In his *Pseudodoxia Epidemica*, which went through several subsequent editions, Browne (1646) refuted, or at least cast doubts upon, many widely accepted beliefs (though, paradoxically, he was a firm believer in witchcraft and in the validity of the Ptolemaic concept of the universe!). Apart from debunking mythical beasts, such as the basilisk (and the amphibaena) Browne made a number of sound observations. Among these he noted that the (soil-associated, adult) earwig, *Forficula auricularia*, is winged, not apterous, as generally supposed. He also noted the occurrence (though not specifically in connection with soil) of the "red-coloured summer spider" or "tainct" (later "taint" or "tant", presumably a trombidid earth-mite, identified by Oudemans (1926) as being *Acarus holosericeus*, described and named much later by Linnaeus (1758) and now the type-species of the genus *Trombidium*. This is probably the first report of a recognizable, free-living, soil-associated mite.²⁰

Before proceeding further, we should perhaps mention here that knowledge of the tropical fauna was increasing at this time. Particularly notable were the writings of Georg Marcgraf, some of which were published posthumously (Marcgraf, 1648; see also Bodenheimer, 1929), though others have only recently come to light. Apart from mentioning the termitophagous activities of the South American ant-eater, various kinds of Brazilian insects are referred to. These included digging scarabaeoid beetles (illustrated with numerous parasitic or phoretic mites on the pronotum) and the jigger flea (*Tunga penetrans*) which affects human feet by way of the soil - as was known to the early Peruvians (*cf.* Morge, 1973) and had been known to Europeans since the early 16th Century (*cf.* Kevan, 1977).

Such reports of this period really belong to an earlier age, and the same is true of the third textbook of entomology to be published, that of John Jonston (1653), a much travelled Silesian physician of Scottish extraction. The book (Fig. 25, 26) was really a combination and condensation of Aldrovandi (1602), devoid of "non-scientific" matter, and Moffet (Moufet,

Formicæ

Ameiſen

Alärov .

Tab xvii

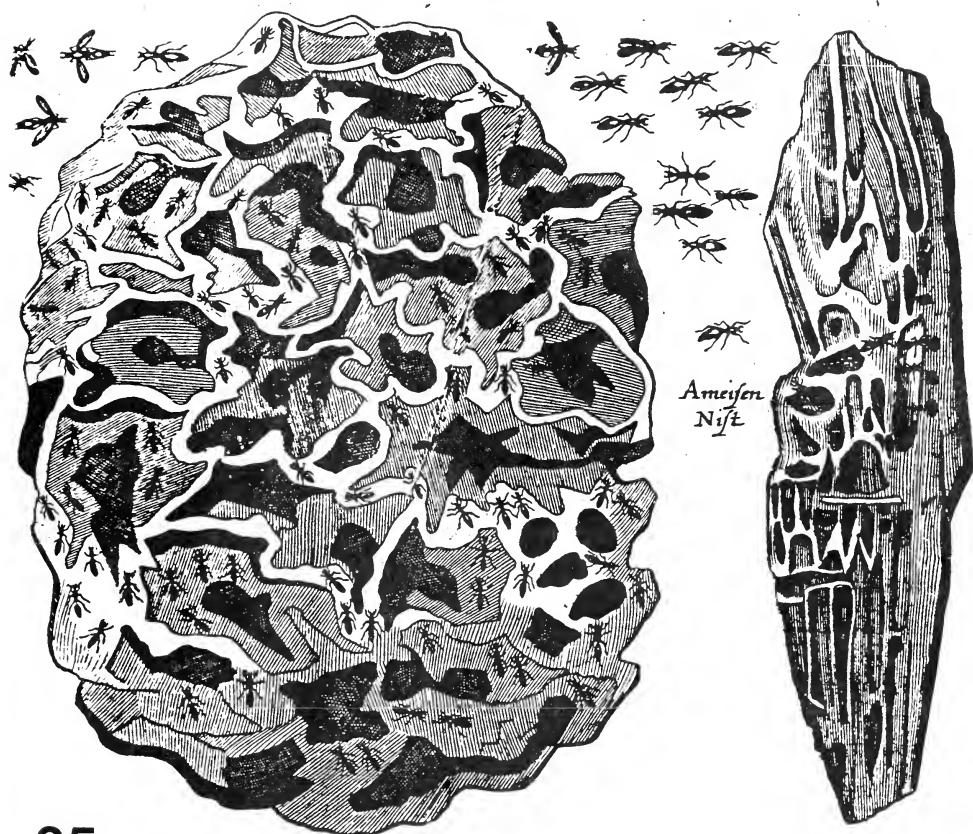
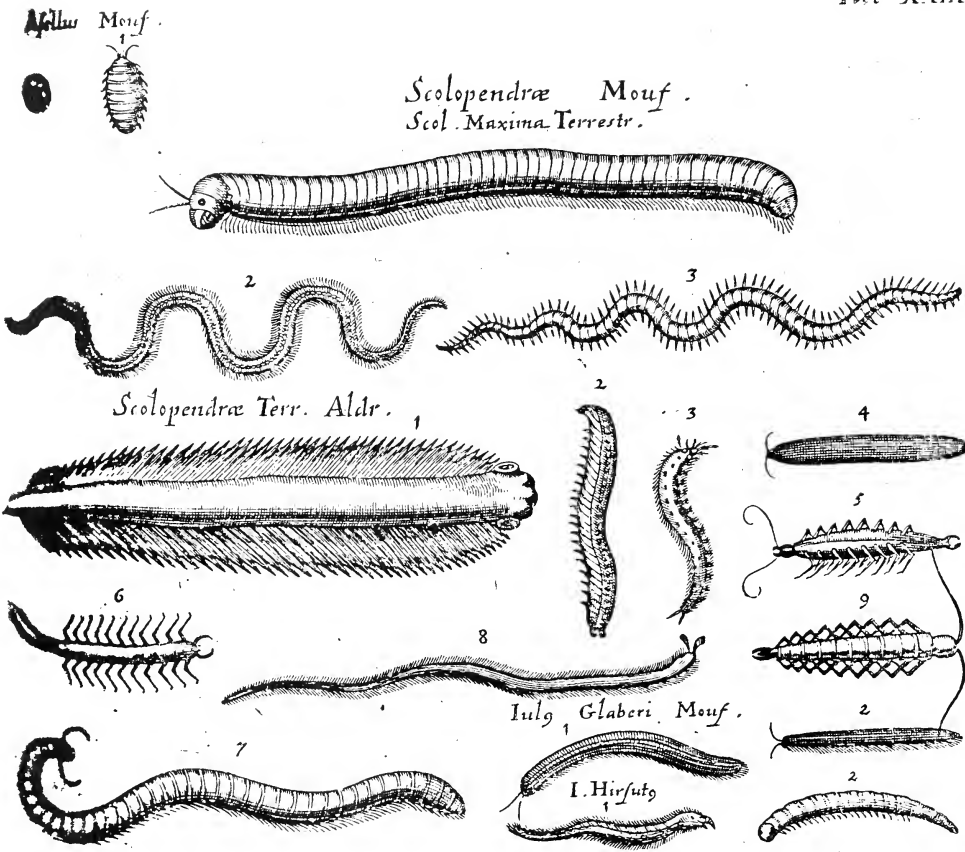


Fig. 25. Ants and their habitations. The upper part of Pl. XVII (opposite p.114) in the third text-book of entomology (Jonston, 1653); from among the illustrations copied from Aldrovandi (1602). [Original in Lyman Collection, McGill Univeristy, Macdonald College Campus.]

1634). It added nothing to what these two authors had included about soil invertebrates. To his volume of four (not three as indicated in his title) "books" on insects, etc., Jonston appended two more, culled from other authors, embracing serpents and dragons. These latter indicated that belief in mythical Mediaeval dragons, basilisks, hydras and so on, were still current, if declining. The "*Amphisboena*" (*sic*) was, however, no longer a two-headed monster (Fig. 26, lower), but had taken its place among rational legless, burrowing reptiles, along with the rather similar "*Scytale*" and "*Caecilia*".²¹

It was shortly after the appearance of Jonston's work that the first free-living nematodes were discovered by Borel (1656). Although these were vinegar eelworms, *Turbatrix aceti*, and not soil-inhabiting, their recognition had very important implications for soil zoology. Fragments of the history of soil nematology will be found in Overgaard-Nielsen (1949) and, to a minor extent, in Thorne (1961) and Chitwood and Chitwood (1974).



Amphisbaena Greuini



Fig. 26. Above, "Asellus" (woodlouse, presumably *Armadillidium*) and "Scolopendrae" (myriapods, including marine polychaet worms) from lower part of Pl. XXIII of Jonston (1653); illustrations taken from Moufet (1634) and Aldrovandi (1602) as indicated. Below, one-headed "Amphisbaena" from upper part of Pl. IV of Jonston's appended book on serpents. [Original as Fig. 25.]

The closing years of the sixth decade of the 17th Century also saw further discoveries in the tropics. Bontius (1658) briefly mentioned a few marginally soil-associated, East Indian arthropods, such as scorpions, cockroaches, ants, scarabaeoid and other beetles. Rochefort (1658), besides cockroaches, discussed West Indian termites (mainly in wood) and the already well-known jigger fleas (*Tunga penetrans*). Piso (1658) noted the occurrence of several root-feeding insect pests of sugar-cane and cassava in Brazil.

Sperling (posthumous, 1661) might now be mentioned, if only for his somewhat novel approach to zoology in presenting the subject as a sort of catechism in the form of statements, questions and answers. Many kinds of insects were referred to, but only the clever, industrious, corn-gathering (!) ants concern us here (*cf.* Bodenheimer, 1928). Goedart (1662, 1667) however, made one or two important observations, and he is generally regarded as being the first naturalist for many centuries to rely mainly on his own observations, rather than on written "authority" (though this distinction might more properly be claimed by Bauhin, 1598, above). Part I of his work (1662) gives a good illustrated account of the biology and ecology of the mole cricket, *Gryllotalpa*, and its subterranean nest and eggs. (Bodenheimer, 1928, who discusses the complex authorship of the work, notes that Goedart claims to have invented the name of the insect.) Part II (1667) contains a very good account of the crane-fly, *Tipula paludosa*, and its leatherjacket larva, correctly suggesting a three-year life-cycle; he also mentions a four-year cycle for the May-beetle (*Melolontha*) with its root-feeding larvae. Part II is also important from the point of view of soil acarology and nematology as it draws attention to, and illustrates for the first time, acariform mites and rhabditiform nematodes (Fig. 27), which are shown in the decaying remains of an ink-cap (*Coprinus*) fungus.²²

An increasing number of relevant observations were made by various authors during the latter part of the 17th Century. Some of these may be briefly commented upon in the form of the following list:

Hooke (1665): described and gave the first good illustration of a cryptostigmatic mite (Fig. 28) associated with mosses and fungi; Oudemans (1926) identified this member of a dominant group of soil organisms as "*Acarus*" *geniculatus*; Hooke (1665), in addition, reporting again on the vinegar eelworm *Turbatrix aceti* (see p. 403), also discovered the nematode *Panagrellus redivivus* that occurs in wallpaper paste, an important prelude to the discovery of species directly associated with soil (*cf.* Goedart, 1667, above).

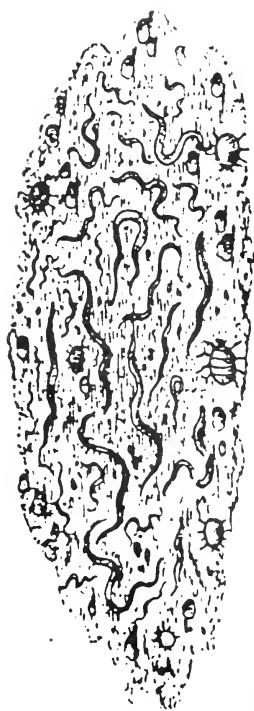
Anonymous (1665): was the first report from North America of cicadas, the holes left by their emergence from the soil, and their exuviae (Bodenheimer, 1929: 159, gives later references also).

E. King (1667): gave a fairly detailed account of the biology of ants, including the pupal nature of "ants'-eggs".

Charleton (1668): made early observations on cryptostigmatid mites on bark (*cf.* Oudemans, 1929); he also commented on various insects, including mole crickets and earwigs, but his information was taken directly from Aldrovandi (1602) and Moffet (Moufet, 1634).

Redi (1668): did not make much direct contribution to knowledge of soil fauna, but exploded the myth of spontaneous generation of insects, etc., from "filth" and other substrates, including soil; he also referred to phoretic mites on ants, both winged and wingless, and on beetles (see Oudemans, 1926; Bodenheimer, 1929).

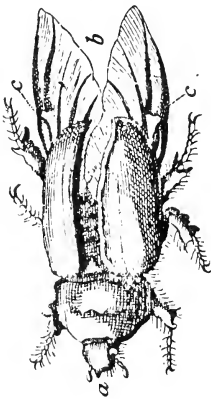
Swammerdam (1669): amongst general observations, noted that certain invertebrates developed without metamorphosis, namely, spiders and mites (probably not soil forms), scorpions, isopods, myriapods, earthworms and slugs. It may also be noted here that, in the



27

TAB: XXVII

Fig. II.



29

Fig. I.



Fig. V.

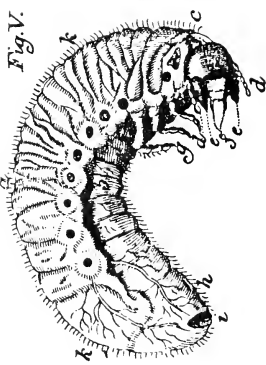


Fig. IV.

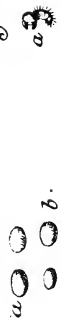


Fig. 1

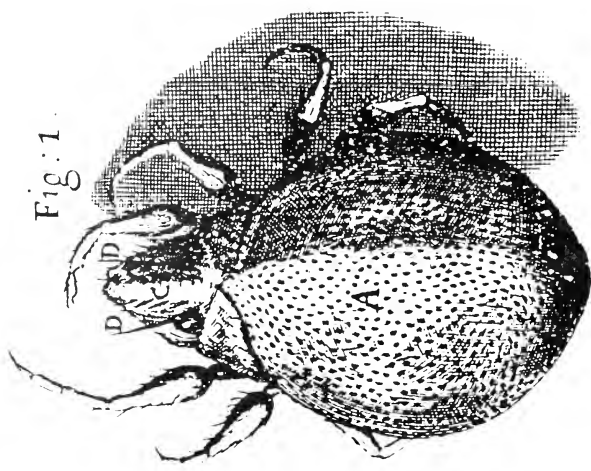


Fig. 27. Acariform mites and rhabditiform nematodes in the decaying remains of an ink-cap fungus, illustrated by Goedart (1667). Fig. 28. The "Wandering mite" illustrated by Hooke (1665); the first good illustration of cryptostigmatid mite, see p. 403. Fig. 29. Adults, eggs and subterranean larvae of the horned scarab "*Nasicornis*," from the upper part of Pl. XXVII of Jan Swammerdam's posthumous *Bybel der Nature* (1737-38), completed by 1670. [Original in Lyman Collection, McGill University, Macdonald College Campus.]

52-years-posthumous *Bybel der Natuure* (Swammerdam, 1737–38), detailed studies on ants and their nests, and illustrations of the horned scarab beetle and its subterranean larva (Fig. 20) were published.

Wray (1670; i.e., the botanist John Ray before he changed the spelling of his name): experimented with formic acid obtained from ants. It may also be noted here that, in 1672, Francis Willughby, who was responsible for most of Wray's later, posthumous, entomological publication (Ray, 1710), died.

Kircher (1675, 1680): attempted to relate "science" with the animals of the *Holy Bible* and to dismiss Redi's (1668) work (above), maintaining that Noah's Ark could not possibly have accommodated representatives of all known living creatures, so that spontaneous generation must be accepted for many; insects, etc., arose from dead material in the proper proportions; six classes of such animals existed; from *soil* came earthworms and slugs, etc., and from excrement and cadavers emerged scarab (and other) beetles (as well as wasps and bees); another group included ants and crustaceans (which would include isopods). [An earlier work of Kircher (who was a Jesuit priest), dating from 1665 and entitled *Mundus Subterraneus* ... (in 12 "books"), and an even earlier one of 1657, with the same words in the title, sound like hopeful sources for the historically inclined soil biologist, but they are basically theological!]

Holger Jacobsen [1676]: as indicated briefly by Petit and Théodoridès (1962: 338) made an important study of the anatomy of the mole cricket (*Gryllotalpa*), presumably in *Acta medica Hafniensis*, but the work is unknown to me and unlisted in the principal entomological bibliographic sources.

Lister (1678): referred to the red trombidid earth mite, called "tant" (*cf.* Browne, 1646, see p. 402), identified by Oudemans (1926) as "*Acarus*" (now *Trombidium*) *holosericeus*, though not actually *in soil*.

Wagner (1680): noted that the cockchafer (*Melolontha*) larva (whitegrub) was called "*Inger*" or "*Enger*" (currently *Engerling*) in German because it curled around roots, no kind of which remained undamaged by them; significantly a three-year subterranean developmental period was said to be required in Switzerland *cf.* a total life-span of four years in the Netherlands, indicated by Goedart, p. 405). The ridiculous practice of excommunicating the beetles, as at Lausanne, in earlier days was also noted (*cf.* p. 389 and Fig. 16).

Claude Perrault [1680]: in *Les Mécaniques des Animaux*, described and discussed the alimentary canal of the mole cricket (*Gryllotalpa*), according to Petit and Théodoridès (1962: 332). He also published a small tract on *Melolontha* (*cf.* Bodenheimer, 1929: 307). Neither of these works is known to me, nor are they listed in the principal entomological bibliographic sources.

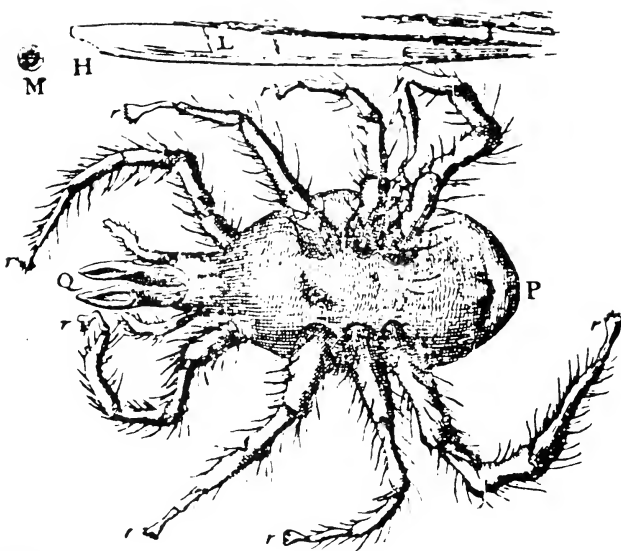
Knox (1681): was for many years a prisoner in Sri Lanka; his entomological observations included pertinent comments on ants of various kinds (some of which excavated large holes in the soil) and particularly on termites, their activities, depredations and mounds; his writings seem to have been ignored in virtually all major termitological literature, but Bodenheimer (1929) quotes him from a German translation of 1689.

Mentzel and Ihle (1683): recorded phoretic mites, identified by Oudemans (1926, 1929) as "*Acarus*" (now *Parasitus*) *coleopttratorum*, on geotrupid beetles.

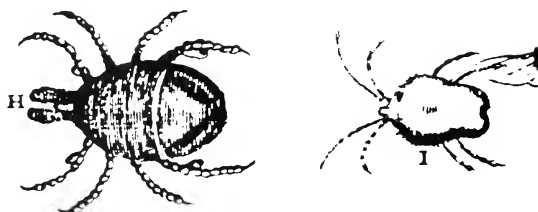
Muralto (1683, 1684): discussed and illustrated the anatomy of the Wood cricket *Nemobius sylvestris*, not a burrower), the Common earwig (*Forficula auricularia*) and, more notably, the mole cricket (*Gryllotalpa*).



30



32



31

Fig. 30. The first (?) recognizable illustration of Collembola (*Hypogastrura* on snow) by Spielenberger (1684). After Bodenheimer (1928). Fig. 31. Early illustrations of mites from Blankaart (1688). H, a species phoretic (?) on soil and other insects, *Parasitus coleoptratorum* (Mesostigmata, Parasitidae), called "Luis van een vliegnet torretje" or "luis van de gekokerde vlieg"; I, Scarlet earth-mite, *Trombidium holosericeum* (Prostigmata, Trombidiidae), called "Schaarlaken-roode Aard-spinneken" or "Scharlaken-Aard-spin." Fig. 32. Phoretic (?) mite, *Parasitus coleoptratorum*, from a geotrupid dung-beetle, illustrated by James Wilson (1702).

Spielenberger (1684): published the first (?) recognizable illustration of Collembola (a species of *Hypogastrura* - Fig. 30) albeit from the surface of snow and not from soil (where Collembola constitute one of the most numerous groups of animals). Insects have been reported on snow since, at least, the times of Aristotēles and Plinius, but here their collembolan nature is undoubted(cf. Bodenheimer, 1929).

Griendel (1687): gave detailed figures of wingless ants and with their pupal "eggs".

Blankaart (1688): reported on various mites (Fig. 31), including those occurring on burying beetles (*Necrophorus*) and a figure of the red trombidiid earth mite, identified by Oudemans

(1926) as "*Acarus*" (now *Trombidium*) *holosericeus*, though again above ground.

Mentzel (1688): illustrated the nymphal stage and exuviae of cicadas (cf. Bodenheimer, 1929).

The anonymous author, referred to by Bodenheimer (1928) as Hohaus (ca. 1690), gave details of the biology and damage caused by mole crickets (*Gryllotalpa*).

Kämpfer [? ca. 1693] (1727–28): recorded observations on termites and ants in the Far East (see Bodenheimer, 1929, who quotes a German version of 1749).

Leeuwenhoek (1695): was most famous for his development of the microscope, with all that that implied for the future study of the soil fauna, but he did not contribute significantly to such studies himself. We may, however, mention his notable, detailed, illustrated account of the biology and ecology of the crane-fly, *Tipula paludosa*, and its root-feeding leatherjacket larva (cf. Bodenheimer, 1928). In this, he "correctly recognized the limiting circumstances of population dynamics" (Beier, 1973). Leeuwenhoek (1697) also made observations on ants, once more commenting on the pupal nature of the so-called "ants'-eggs". Each of these contributions, however, had been largely anticipated some 30 years previously by Goedart (1667) and E. King (1667) respectively (see p. 405).

Camerarius (1699/1700): again referred to Collembola on snow (cf. Spielenberger, 1684, above).

Carrying forward the selected list of "soil fauna" publications into the 18th Century, we may note the following:

Wilson (1702): gave a good illustration (Fig. 32) of a mite (*Parasitus coleopratorum*) from geotrupid dung-beetles.

Poupart (1704): described, for the first time, the life-history of the unusual rhagionid fly *Vermileo vermileo*, the "ant-worm", whose pit-dwelling larvae live in a similar manner to those of myrmeleontid Neuroptera (true ant-lions).

Wilhelm Bosman [1704] of the Dutch East India Company resident in Guinea, according to Bodenheimer (1929), quoting a 1708 German version, refers in his "Voyage to Guinea ..." to ants and to termites; the former he believed had a language; the latter were said to build mounds twice as tall as a man [not an exaggeration], but he did not know if they had a "king" as big as a [full-grown] fresh-water crayfish, as a Mr. Foquenberg would have it. [The queens of some *Macrotermes* species are indeed almost as large as indicated.]

Sloane (1707): published the first of his two volumes on West Indian natural history, but only the second of these is relevant here, and this did not appear for many years (Sloane, 1725), see p. 411).

(W)ray [and Willughby] (1710) published (posthumously *per* Martin Lister) an early classification system for "insects" (i.e., terrestrial invertebrates) that began a trend towards orderly taxonomy. What might be termed soil fauna was included in the following categories:

I. "Ametamorphata" (without change)

A. 1, a: legless land animals living in earth - "*Lumbricus*" (all earthworms), slugs.

B. 1, a, x: 6-legged land animals (larger) - probably beetle larvae.

xx, yy: ditto (smaller not holding on to other animals) - including collembola, "booklice" and some other dubious forms.

2, a: 8-legged, with tail - "*Scorpio*"

b: ditto, without tail - "*Araneus*", "*Opilio*", ticks, mites

- 3: 14-legged - "*Asellus*" (isopods and amphipods)
- 4: 24-legged - ? "bristletails"
- 5, a: Many-legged land animals - myriapods

II. "Metamorphumena" (making a change)

- A. No resting pupal stage - "*Gryllus*", "*Gryllotalpa*", "*Cicada*", "*Forficula*".
- B, 1, a: Moults to pupal stage visible, Coleoptera or Vaginipennia - "*Scarabaeus*" (= all beetles except staphylinids)
- 2: Moults to pupal stage concealed - "*Muscae*" (higher Diptera)

This work also included reference to mites infesting ground beetles and Lister's appended *De Scarabaeis Britannicis* including Scarabaeoidea, Carabidae, Elateridae and Staphylinidae) and classification of British "insects".

Réaumur (1713 ?): recorded *Parasitus* mites on geotrupid dung beetles (and on bumblebees, etc.) - cf. Oudemans (1926).

Vallisneri (1713): had a classification system in which his third major group of "insects" comprised those that lived in the earth and in hard substances, but this was not adopted in his later, major work of 1773 (see Bodenheimer, 1928).

Günther (1718, 1719): in a sort of quarterly almanack, referred to cockchafers (*Melolontha*, mainly swarming adults), mole cricket (*Gryllotalpa*, illustrated as having a curious proboscis), and cutworms (*Agrotis* and other noctuid caterpillars damaging vegetable roots, illustrated). A little later (Günther, 1723), he again refers to cutworms attacking roots, and to ants (cf. Bodenheimer, 1928, 1929).

Kolbe (1719): included reference to termites in South Africa.

Frisch (1720, 1722, 1727, 1736): in parts of a serially-published work on mainly economic aspects of entomology in Germany, made, near the beginning, observations on (burrowing) field crickets (*Gryllus campestris*), recommending their use in biological control of House crickets (*Acheta domesticus*); these, he suggested, would be driven out by their more aggressive cousins. Although this was not a practical proposition, he properly stressed that control of pests was not possible without adequate knowledge of their biology, the biological control of crickets being an example of this. Among the few soil pests considered by him was (1727) the crane-fly *Tipula paludosa*. The subterranean larvae of the Rose chafer, *Cetonia aurata*, were mentioned in the 12th part of the work (1736). Frisch (1772) also records various uropodid and gamasid mites on beetles (including Geotrupidae) in dung (see Oudemans, 1926).

Sloane (1725): in the delayed second volume of his work (see p. 409), discussed various insects associated with soil in the West Indies (mainly Jamaica), notably ants, termites, rootgrubs (scarabaeoid larvae) and the jigger flea (see also Kevan, 1977).

Linnaeus (1735): published the first, short, but regal-folio edition (Fig. 33) of what eventually, in a different form, was to revolutionize many aspects of natural history, his *Systema Naturae*. In it he distinguished the following animals that one may associate with soil:

I. QUADRUPEDIA: Ferae - *Talpa* (mole). Glires - *Sorex* (shrew).

III. AMPHIBIA: SERPENTIA (*Corpus apodum* ...) - *Anguis* ("snakes", including *Caecilia*); here Linnaeus notes some fabulous monsters (e.g., Dragon and Basilisk, but not

C A R O L I L I N N Æ I, *SVECI*,
 D O C T O R I S M E D I C I N Æ,
 S Y S T E M A N A T U R Æ,
 S I V E
 R E G N A T R I A N A T U R Æ
 S Y S T E M A T I C E P R O P O S I T A
 P E R
 C L A S S E S, O R D I N E S,
 G E N E R A, & S P E C I E S.

O JEHOVA! *Quam ampla sunt opera Tua!*
Quam ea omnia sapienter fecisti!
Quam plena est terra possessione tua!

Psalm. civ. 24.

L U G D U N I B A T A V O R U M,
 Apud T H E O D O R U M H A A K, M D C C X X V.

E X T Y P O G R A P H I A
 J O A N N I S W I L H E L M I P R I N T G R O O T.

33

Fig. 33. Title page of Linnaeus' (1735) first (regal-folio) edition of the *Systema Naturae*.

Amphisbaena).

V. INSECTA: Coleoptera - *Forficula* ("Staphylinus" or cockroach!, and *Auricularia* or earwig), *Scarabaeus* (including *Scarabaeus pillularis* and *Melolontha*), *Carabus* (including "*Cantharellus*" *auratus*). Hemiptera - *Gryllus* (only "*Gryllotalpa*" is of present concern), *Formica* (ants), *Scorpio* (*S. terrestris*, as opposed to "*S. aquat.*" or *Nepa*; Linnaeus obviously did not know a true scorpion and deduced their taxonomic position from old descriptions). Aptera - *Acarus* (ticks, mites, etc., including *Pediic[ulus]* *Scarabaei* [on beetles] and *Scorpio-araneus*, pseudoscorpions), *Araneus* (spiders, etc., including "*Tarantula*" and also *Phalangium*), *Oniscus* ("*Asellus*" spp., isopods), *Scolopendria* (including *Scolop. terrestris* or centipedes, "*Scolop. marina*" or polychaete worms, and *Julus* or millipedes).

VI. VERMES: Reptilia - *Lumbricus* (including *intestinum terrae*, Aristotēles' name in Latin for earthworms, *L. latus* and the parasitic nematode, *Ascaris*), *Limax* (slugs).

Subsequent editions before the 10th (Linnaeus, 1758) need not concern us here.²³

Réaumur (1738): made references to, and illustrated, various dipterous larvae, including some living in soil; he gave a rather full account of the life-history of the Narcissus bulb-fly, *Merodon equestris*; he also figured ant-lion larvae. Continuing his entomological *Mémoires* (Réaumur, 1740), he gave illustrated accounts of crane fly (*Tipula paludosa*) and a bibionid (? *Bibio hortulans*) and their subterranean larvae; he also discussed and illustrated "*Cicada orni*" and its nymph. A little later, Réaumur (1742) illustrated the life history of "*Formica-leo*" the ant-lion (Fig. 34); he also mentions the well known phoretic mite *Parasitus coleoptratorum*, though not on beetles (cf. Oudemans, 1926). Réaumur never published the last four projected volumes of his work, although his manuscripts are preserved in Paris and part of his sixth volume, written about 1743-44, and dealing with ants, was published posthumously (Réaumur, 1926).²⁴

Geer (1740, 1743): for the first time, adequately described and discussed Collembola; he also gave good illustrations (Fig. 35), though these were not the first for the group, as has been stated by some (see Spielenberger, 1684, and p. 407). His specimens were found in winter on tree-bark, but this does not detract from the importance of his contribution on these typical soil hexapods. He observed their method of springing, their moulting, their exuviae, their eggs, and the presence of the unique ventral collophore.

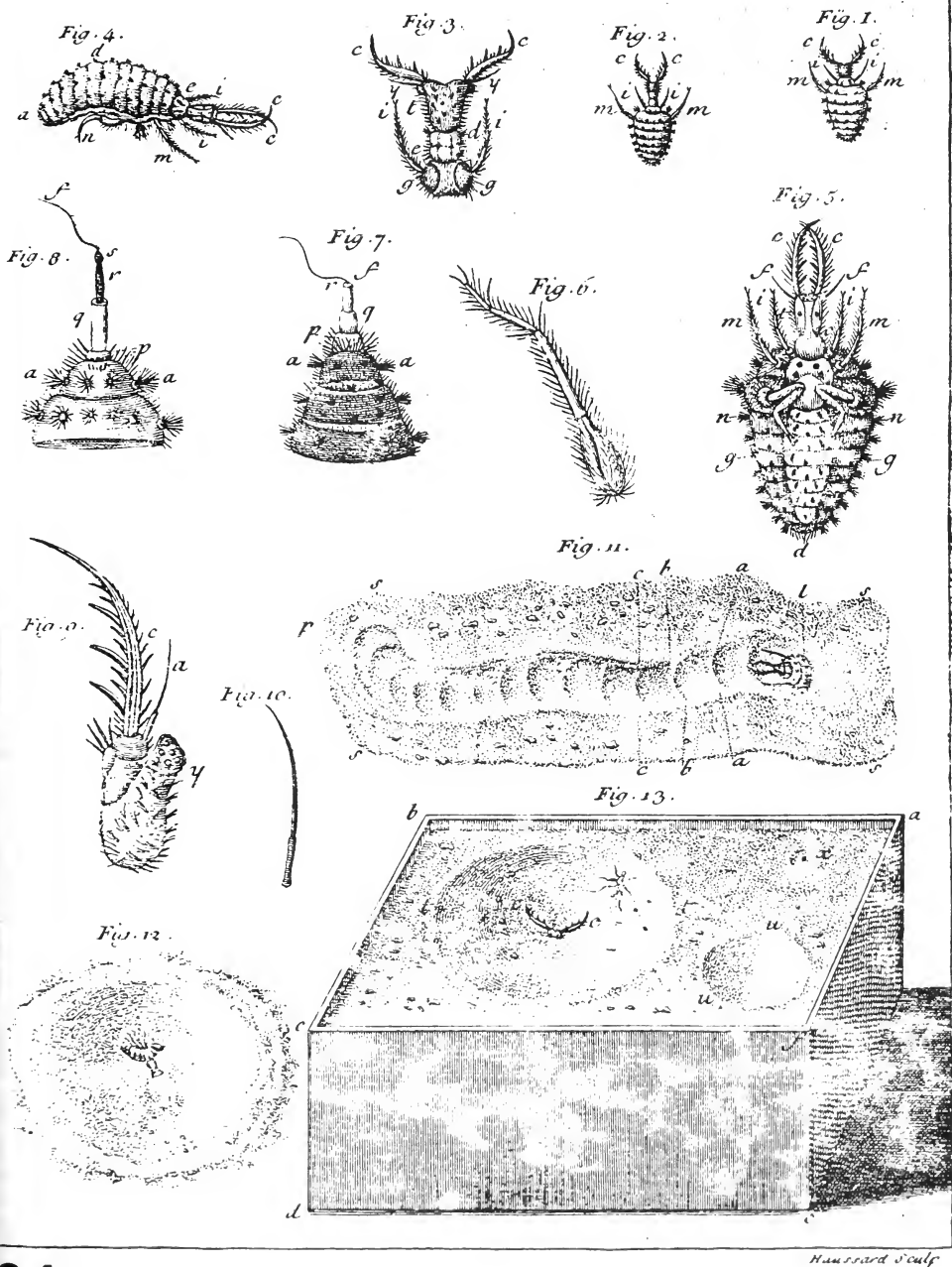
Linnaeus (1741): unlike Swammerdam, recognized winged male from winged female ants.

Baker (1743): reported mites on earwigs and geotrupid dung-beetles (*Anoetes polypori* and *Parasitus coleoptratorum* respectively; cf. Oudemans, 1926; Bodenheimer, 1929).

Needham (1743, 1745): identified the nematode *Anguina tritici* that causes "ear-cockle"²⁵ in wheat (see also Thorne, 1961). This was the first plant-parasitic nematode to be discovered and, though the "cockle" galls occur in the ears of panicles of grasses, they fall to the ground and the worms pass a significant part of their lives in the soil. The importance for soil zoology of this discovery, therefore, was considerable.

Linnaeus (1745): reporting on his trip to Oeland and Gothland in 1741, mentioned carabid, staphylinid and scarabaeoid beetles, ants and "ant-lions" (larvae of *Myremeleon*). His *Fauna Suecica* (Linnaeus, 1746), following the classification of his *Systema Naturae* (above), referred, amongst soil-associated animals, to mole crickets (*Gryllotalpa*) as garden pests, and to various other root-feeding invertebrates, such as slugs. The depredations of root-worms, presumably the larvae of the swift moth *Hepialis humuli*, attacking hops were noted (see also Bodenheimer, 1929). He also noted phoretic mites (such as *Parasitus coleoptratorum* and

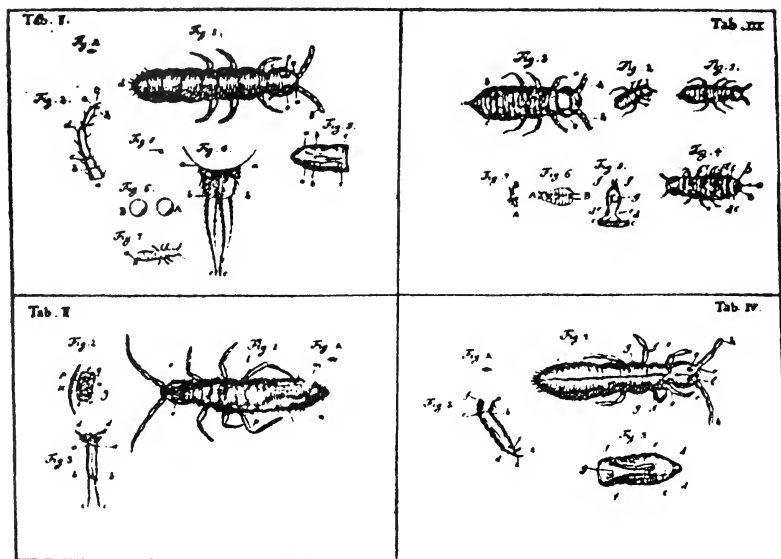
Pl. 32. pag. 386. Mem. 10. de l'Hist. des Insectes. Tom. 6.



Haustrard sculp.

34

Fig. 34. The life history of the "Formica-leo" (*Myrmeleon formicarius*) from *Mémoires pour Servir à l'Histoire des Insectes*. VI. (Réaumur, 1842: pl. 32). [Original in Lyman Collection, McGill University, Macdonald College Campus.]



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Fig. 35. Geer's (1740) early illustrations of Collembola (see p. 412).

Uropodidae) on geotrupid dung beetles and other Coleoptera, and the red earth-mite (*Trombidium holosericeum*) and other mites within the soil ("habitat in terra") - see Oudemans (1926). This may, indeed, be the first record of mites actually in soil. The prostigmatid mite, now known as *Achiptera coleoptratus* was recorded from under stones ("sub lapidibus").

Gould (1747): in his account of English ants, gave information on the biology of several species; he also stated that ants are eaten by mole crickets (as well as by other enemies) and noted that millipedes and earwigs, in particular, are among the commensals inhabiting ant nests.

Baker (1747): gave an account of the damage to pastures in eastern England by whitegrubs and cutworms.

Rösel (1749): included fine engravings and accounts of the mole cricket and field crickets.

Hughes (1750): referred to field crickets (*Gryllus assimilis*) under stones and lumps of earth in Barbados; he also discussed ants and termites there.

Hill (1752): recorded red earth mites, presumably *Trombidium holosericeum*, as being "very common under surface of earth", as was apparently the "grey rough earth acarus," a cryptostigmatid mite determined by Oudemans (1926) as "*Acarus scaber*," possibly a species of *Cepheus*, and "the little black Acarus," *Pergamassus crassipes* (cf. Oudemans, 1929).

Geer (1752): gave another account of the rhagionid dipteran *Vermileo*, the "ant-worm fly" referred to much earlier by Poupart (1704), see p. 409.

Réaumur (1753): gave yet another illustrated account of the same insect.

Rösel (1755): described true ant-lions (Myremeleontidae) and illustrated his account with engravings very similar to those of Réaumur (1742, see p. 411), but of even higher quality. Rösel died in 1759, but some time prior to that he had prepared material for his fourth volume.

(Rösel, 1761) which showed phoretic mites on *Necrophorus* burying beetles (cf. Oudemans, 1926).

Kalm (1756a): gave a very comprehensive account of the "17-year" cicada (as "Gras-Hopper") in eastern North America. The same author (Kalm, 1756b, 1761) again referred to the same insect and to field crickets, *Gryllus "niger..."* (mostly *G. pennsylvanicus*, sometimes *G. veletis*), the latter overwintering in the soil, on one occasion at a depth of "ten inches" (not piled up to that depth on the surface as mistranslations imply). Kalm is one of the earliest authors to state that he actually dug for invertebrates in the soil! Among the overwintering insects that he found beneath the surface were various kinds of ants, carabid and scarabaeoid beetles and their larvae (including June-beetles and whitegrubs, geotrupids and horned scarabs). Native, litter-dwelling (as well as imported, domiciliary) cockroaches are also mentioned. Kalm's so-called woodlice, however, were not isopods but ticks.

Osbeck (1757): commented upon several kinds of "*Scarabaeus*" beetles and the substrates in which they occurred in Spain. Reference is also made to Spanish field crickets (see also Bodenheimer, 1929).

Adanson (1757): observed various insects during his sojourn in Senegal, and among these were termites (cf. Bodenheimer, 1929). Apart from noting their destructiveness, describing fruitless efforts to combat their ravages, suggesting arsenic and fire for the purpose, he also made observations on the internal structure of termitaria. He was astute enough to conclude that the majority of the termites that were most destructive to his possessions were not of a kind that build conspicuous mounds; he noted their covered galleries. Reading Adanson, one gets the impression, perhaps for the first time, that here was an author who had some appreciation of the intricate association between the soil and its (termite) fauna.

We have now reached that point in zoological history, when Linnaeus (1758) published the 10th edition of his *Systema Naturae*. There was, indeed, no momentous biological discovery associated with this event, but the almost universal adoption of binominal nomenclature for all animals, which followed within a remarkably short time, ushered in a new era. So far as the soil fauna was concerned, the only immediate impact was to add a few more generic names to those listed in earlier editions of the work (and eventually to provide a reference point for validating the various names in the future). Additional, marginally soil-associated genera of Coleoptera included such as *Hister*, *Silpha*, *Elater* and *Staphylinus* (in its current sense, no longer a cockroach). We also find additions such as *Termes* (now specifically meaning termites) and the burrowing Field cricket, *Gryllus campestris*.

To conclude this section, we might just mention one, rather quaint but relevant agricultural work that really belongs to an earlier period, though published in the following decade. This is the poem, written in the early 1760's on St. Kitts, West Indies, entitled *The Sugar Cane* (Grainger, 1764). Kevan (1977) has extracted and commented on all the numerous invertebrate animals mentioned in it. These included a number of soil-related forms, such as burrowing land-crabs (*Cardiosoma*), scale insects on cane roots, ants, termites, crickets, cockroaches, jigger fleas and the human hookworm among the parasitic nematodes.

UP TO THE MIDDLE OF THE 19TH CENTURY

After the publication of the "Tenth Edition" of Linnaeus (1758), a new, if not universal, orderliness came about the field of zoology. While anatomical and biological studies increased, it was, nevertheless, the discovery and description of previously unknown, or unrecognized,

creatures that occupied most attention and which went ahead by leaps and bounds. The "pre-Darwinian" systematic era had begun! Author after author added more and more species to the known fauna of the world, and, though the proportion was not large, many of the animals involved were associated with the soil and litter, if not as adults, then in their immature stages.

Clearly it would be profitless to attempt to enumerate in detailed succession the new discoveries in the manner I have adopted hitherto in this review. We must confine our attention to the more significant events for soil zoology and to the relevant publications. For the general trends of the period, with many specific examples from entomology (though few mention the soil fauna even indirectly), the reader is referred to Tuxen (1973), who begins a little earlier, and to Lindroth (1973), who ends a little later than does this section. For an exhaustive account of developments in acarology from 1759–1804, see Oudemans (1929). A full bibliography of the literature on oligochaet annelids (including terrestrial forms) to 1894, is given by Beddard (1895); Stephenson (1930) gives no historical review for these creatures; Reynolds and Cook (1976) limit their brief remarks to taxonomy.

Before proceeding further, however, we should remember that there were, of course, others than Linnaeus himself who crossed the "nomenclature boundary", and amongst these, perhaps the most important was his compatriot Karl De Geer, whose *Mémoires pour servir à Histoire des Insects* (so called in deference to the works of Réaumur, p. 411, and published in Stockholm) began in 1752, *before* the "Tenth Edition". The final volume, the seventh, however, was not published until the year of its author's death, 1778. It was in this volume that Geer's early observations on Collembola (see p. 413) were reprinted. The series did, of course, contain many references to various other soil- and litter-associated insects, etc., but we shall not enumerate these, other than, perhaps, to mention "*Acarus vegetans*", a uropodid mite on staphylinid beetles noted in 1768 (Oudemans, 1929).

In this period, we should also refer to the general entomological publications of such other authors as J.C. Fabricius, P. Rossi, P.-A. Latreille, W. Kirby and W. Spence, and H.C.C. Burmeister, to mention but a few. The first of these published his most important works from 1775 to 1798, but we shall mention only his *Philosophia Entomologica ...* (Fabricius, 1778). This is because that particular work is regarded by some as being the first *real* textbook of entomology, dealing as it did, with the subject scientifically and confining itself to non-marine arthropods. Rossi is included here, not only for his important example of work on localized faunas, his *Mantissa Insectorum ...* (Rossi, 1792, 1794), but more because he was the first ever Professor of Entomology to be so designated (at the University of Pisa, 1801–1804). He did not, in fact have much direct connection with soil fauna, but the recognition of entomology as a discipline was to be of major importance to its study. Latreille's numerous revisions of the classification of arthropods, mainly between 1802 and 1829, are also of major general significance, but, from a "soil" point of view, he also devoted much time to the study of ants (Latreille, 1802).

Kirby and Spence (1815–1826) made an outstanding contribution to entomology by "popularizing" the subject without degrading it. Nevertheless, they contributed little or nothing beyond what was already known to the knowledge of the soil fauna as such. Admittedly, in the first volume (1815 [& 1816]), they considered certain soil-inhabiting species amongst the pests about which they wrote, but they added virtually nothing new. Similarly, in their second volume (1817), though they devoted 75 pages to ants and termites, they limited discussion almost entirely to their biology and behaviour, with little, if any, indication of the possible roles of these insects as part of the soil fauna.

Towards the close of the period treated in this section, Burmeister (1832) published the first (general introductory) volume of his influential *Handbuch der Entomologie*. His final (5th) volume did not appear until much later, in 1855.

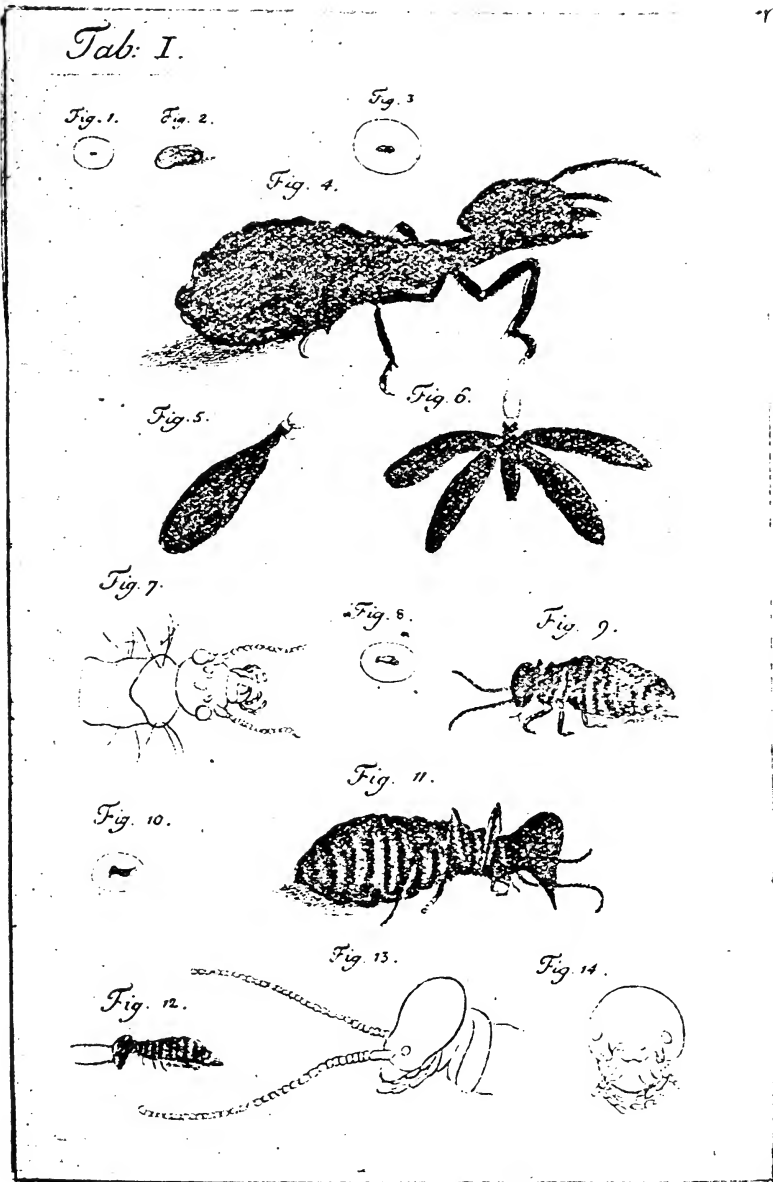
We might now mention a few publications of more particular interest (direct or indirect) for a study of the soil fauna, that appeared during the period considered here. We may begin by noting Spallanzani's (1769) account of free-living nematodes, to which he again referred many years later, in 1787 (*cf.* Chitwood and Chitwood, 1974). Two references by O.F. Müller (1773, 1776) are also notable as they were the first to recognize the distinctness of that extremely important group of soil animals, the enchytraeid oligochaet worms. "*Lumbricus*" (now *Lumbricillus*) *lineatus* and "*L.*" *minutus* (of dubious identity) were the species involved, both from near the seashore (*cf.* Reynolds and Cook, 1976, who give a brief history of oligochaet research generally). Also concerned with "worms," once more with the "ear-cockle" nematode of wheat, *Anguina tritici*, we may also mention Roffredi (1775) and Scopoli (1777), who, respectively, began to unravel the life-history, and named the genus, though not the species. [The latter was not done until Steinbuch (1799) worked mainly on a related species, *A. agrostis* - see Thorne (1961).]

In the meantime, Schrank (1776, repeated 1781) was writing about mesostigmatid mites, such as *Pergamasus crassipes*, and Collembola, like *Onychiura ambulans*, in soil under flower-pots, and mites like *Hologamasus lichenis* under lichens (see Oudemans, 1929); and O.F. Müller (1786 - *cf.* Chitwood and Chitwood, 1974) made the first observations on truly free-living fresh-water nematodes (many of which may occur in the water-film around soil particles).

Another group of predominantly soil-inhabiting animals that were written about quite extensively by European travellers to the tropics were termites. Notable among such authors were König (1779) in respect of southern India and Sri Lanka (Fig. 36), and Smeathman (1781) regarding tropical West Africa (Fig. 37). Fletcher (1922) translated König's paper and commented upon that of Smeathman; Thakur (1984) briefly notes that König was probably the first author to investigate termites *scientifically* in Peninsular India and Sri Lanka (though there had been much earlier reports from the latter by Knox, p. 407), and he clarifies the nomenclature. Fungus-gardens, ectoparasites, the use of termites as human food, etc., are all mentioned. Sparrmann (1784) [1783] also wrote about termites in Africa, but in respect of South Africa. Among other things he observed their "piercing the soil."

More significant, perhaps, and published a few years later (though mostly written earlier) came the first edition of *The Natural History and Antiquities of Selborne* (G. White, 1789). In this, White (see also Note 26, p. 440) not only made keen observations on mole crickets (Fig. 38), field crickets, harmful scarabaeoid and tipulid larvae, other insects and injurious slugs, but stated that "worms seem to be great promoters of vegetation which would proceed but lamely without them, by boring, perforating, and loosening the soil, and rendering it pervious to rains and the fibres of plants, by drawing straws and stalks of leaves and twigs into it; and most of all, by throwing up such infinite numbers of lumps of earth called worm-casts, which, being their excrement, is a fine manure for grain and grass ... the earth without worms would soon become cold, hard-bound, and void of fermentation; and consequently sterile ..."²⁶ Here, then, we finally see the beginnings of a clear understanding of the interaction between the soil and its inhabitants!

Nevertheless, though the book was an immediate best-seller (and was even published within three years in a German translation in 1792, the year before White died), this particular piece



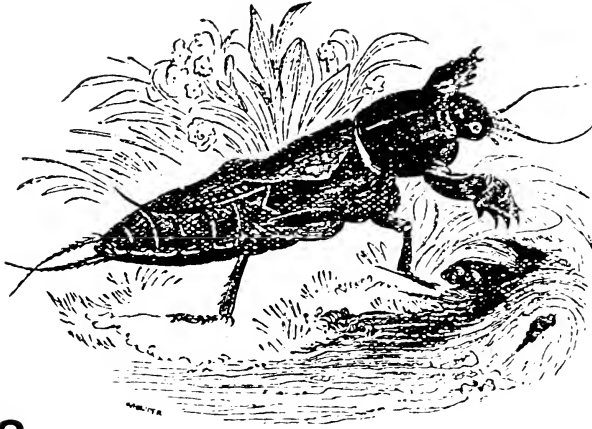
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Fig. 36. Termites from south India and Sri Lanka illustrated by König (1779). Nos. 10 and 11 are of *Hospitalitermes monoceros* (König), from Sri Lanka; nos. 12–14 are of *Anacanthotermes viarum* (König), from South India; the others are of uncertain identity.



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Fig. 37. The illustration of the large, mound-building West African termite, *Macrotermes bellicosus*, from Smeathman (1781). Smeathman tells us that, in certain "English" parts of West Africa, termites had the dubious distinction of being dubbed "Bugga Bug"!



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Fig. 38. Mole-cricket (*Gryllotalpa*). Illustration from an early edition of Gilbert White's (1789) *Natural History and Antiquities of Selborne*.

of wisdom was not followed up for almost half a century, except for the plagiarism by Bingley (1803 and subsequent editions, see Note 26), until Charles Darwin read a paper on the subject to the Geological Society of London on November 1st, 1837, soon after his return from his famous voyage with H.M.S. *Beagle* (Darwin, 1840). — And that did not arouse much immediate interest either!

Meanwhile, general systematic and biological works like those on ants by Latreille (1802) and Huber (1810), and on mites by Schrank (1803–04) and Hermann (1804), went on; Morren (1829) was experimenting with water relations of earthworms; Henle (1837) described the terrestrial oligochaet genus *Enchytraeus* (type species *E. albidus*) from decaying seaweed, sewage beds and compost heaps; Bourlet (1839, 1841, 1842) and Nicolet (1841, 1847) had begun to lay the foundations for the study of important group of soil organisms, the Collembola; and Koch (1835–38, 1844, 1847) did the same for myriapods (and other non-insect arthropods). One may note, too, that Dujardin (1842) wrote about Nematomorpha (gordioid worms) and larger mermithid nematode parasites of insects (his new genus *Mermis*), which can be associated with soil; and then later (Dujardin, 1845), while dealing chiefly with endoparasitic helminths affecting vertebrates, he referred to free-living, soil-inhabiting rhabditiform nematodes, as well as to the plant parasite, *Anguina tritici*. Hoffmeister (1842–45), too, was beginning to distinguish between various species of lumbricid earthworms.

By this time, however, Ehrenberg (1837) had published his tract on the “living soil”, drawing attention to the possible role of protozoa and other micro-organisms therein, and Darwin (1840) had pointed the way to the scientific study of earthworms. Thus, soil biology, as such, may now, perhaps, be said to have begun at last, however modestly. One should not, however, be misled by the title of a paper by Schiödte (1849), “Specimen faunae subterraneae”, for this, though an important landmark of its own, dealt with cave-dwelling, not soil invertebrates.

1850 TO 1900

By the middle of the 19th Century, real knowledge of the soil fauna as such was, in general, only a little advanced from what it had been in the days of Aristotēles. Larger or more conspicuous animals that inhabited the soil were reasonably familiar - such as moles, legless lizards (even true amphisbaenids!) and amphibia, earthworms (though most of these were simply lumped together as "*Lumbricus*", certain slugs, isopods and myriapods, and a modest array of larger insects, such as scarabaeoid and various other beetles and their larvae, cutworms, cicada nymphs, ant-lion larvae, mole crickets and burrowing field crickets, crane-fly, bibionid and other fly larvae, and, of course, various kinds of ants and termites. Incidental knowledge had, however, begun to accumulate regarding smaller creatures, such as Collembola, mites (especially those that lived on insects), enchytraeid worms and nematodes, though mostly as little more than curiosities. Beyond the earthworms, and possibly ants and termites, there was little concept of a soil-fauna community. Other animals were considered largely in isolation, Ehrenberg's (1854) atlas of soil inhabiting protozoa, etc., being an exception.

A noteworthy early contribution to nematology, including free-living forms, was that of Diesing (1850-51), later revised (Diesing, 1861). Also in relation to nematodes, a note by Berkeley (1855) was of considerable interest as it focussed attention on an unidentified "vibro" attacking the roots of cucumbers, probably the first discovery of a plant-parasitic eelworm other than those causing ear-cockles of cereals and wild grasses (*Anguina*), which had again received attention shortly before by Hardy (1850). [J. Kühn's (1857) *Anguillula* (now *Ditybachus*) *dipsaci* on teasel is often considered to be the "second" plant-parasitic nematode.]

Termites were also receiving further attention from a systematic point of view with the first monograph on the group by Hagen (1855-60), while more information on soil-inhabiting nematodes continued to accumulate. For example, Schulze (*in* Carus, 1857) described the soil-inhabiting *Diplogaster micans*; Gervais and Beneden (1859) gave us more on the ear-cockle eelworm (*Anguina tritici*); H.J. Carter (1859) mentioned tropical free-living nematodes while writing on parasites of humans and, economically very importantly, Schacht (1859) noted the occurrence of the cyst-forming, root eelworm (*Heterodera schachtii*, though not then named²⁷) on sugar-beet. Claus (1862) and Eberth (1863) also contributed to our knowledge of free-living nematodes, by which time, however there were only about 80 species known, most of them marine (Overgaard-Nielsen, 1949). Lest it be thought that no progress was being made at this time in the area of integrated soil biology, one should mention here the writing of Post (1861-62), who again drew attention to the important role of living organisms in the soil, but the time was not yet ripe for detailed investigations of this kind. More traditional work of importance during the immediate period was the initiation of the continuing work of Schiødte (1861-83) on the larvae of Coleoptera, very many of which live in soil or litter, decaying vegetation, etc., and which were largely unknown at the time. Koch (1863) also (posthumously) laid the foundations for a better understanding of the myriapods. (His son continued in this field later).

A real beginning was also made on a concerted study of free-living nematodes (including many soil forms) by Bastian (1865). Schneider's (1866) monograph on nematodes in general also appeared about the same time, but it was Bütschli (1873) who provided the basis for the present-day classification of free-living nematodes, of which he included 61 soil and fresh-water species, 30 new (Overgaard-Nielsen, 1949). An interesting discovery was also made about this

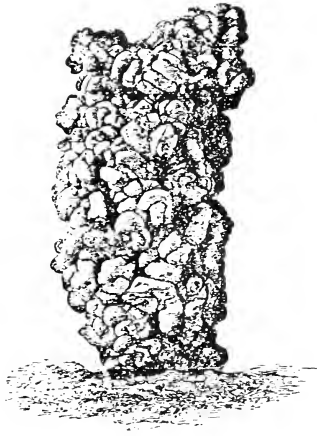
time, when Lohde (1874) first observed nematode-trapping fungi in the soil. Then came the first of J. G. de Man's publications dealing specifically with soil nematodes (Man, 1876), of which he described about 50, most new (Overgaard-Nielsen, 1949). This author continued to publish on free-living species until 1921 (Thorne, 1961). Interest in terrestrial annelids, especially earthworms, was increasing about this time, as indicated by the works of Eisen (1871–1873), who was to continue with their systematics for many years, and of Perrier (1872, 1874), who also did some experimenting with them.

A milestone belonging to this period, for students of the soil fauna, was the publication of the *Monograph of the Collembola and Thysanura* (which included Microcoryphia and Diplura) by Lubbock (1873).²⁸ Such biological and ecological information as was available was included, though it was mainly a systematic work, as was customary (but necessary) at the time. By the end of the decade, Plateau (1876) had studied digestion in myriapods; Hensen (1877) had published the first important paper on the role of earthworms in soil fertility since Darwin (1840); Vejdovský (1877, 1879), in two works, with which I am unfamiliar, began to put the enchytraeid annelids in order; and P.E. Müller (1879), who invented the terms "humus form", "mull" and "mor", stressed that these latter were biological, not merely physico-chemical, systems, in which the fauna in general (not merely earthworms), together with other organisms, was intimately involved (see also P.E. Müller, 1884, 1889).

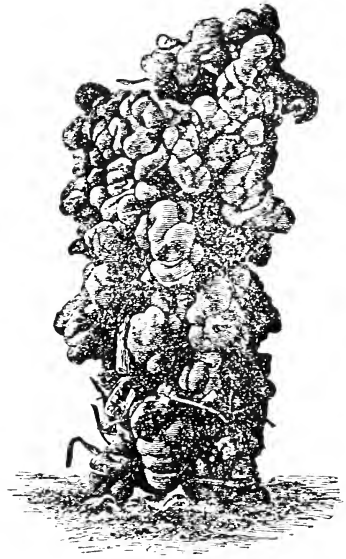
Darwin (1881), with his customary procrastination, now published *The Formation of Vegetable Mould through the Action of Worms* (Fig. 39), which over-shadowed other valuable but slightly later contributions on the subject by Hensen (1882) and Baur (1883). Vejdovský (1885) also made further studies of earthworms and other oligochaets (but not much on Enchytraeidae as he had already dealt with these, as noted above). It is probable that Darwin's book, rather than stimulating further research on the interaction of fauna and soil, tended, by its authoritativeness, to give the impression that there was little more to be said on the matter - except where earthworms were rare or absent. Drummond (1887, 1888) developed the hypothesis that termites were the tropical analogues of earthworms, but soil fauna studies as such did not burgeon forth as might have been expected.

We should now turn our attention again to other groups of animals that are extremely abundant in the soil, namely the myriapods and the mites. In respect of the former, Latzel (1880, 1884) published a very important monograph for central Europe. Knowledge of mites was gradually accumulating as a result of the efforts of various authors, but one in particular, Antonio Berlese, should be mentioned. His *Acari, etc.*, in Italia reperti, published over many years (Berlese, 1882–1903) included large numbers of soil-inhabiting species. Before his major contributions were made²⁹, however, Michael (1884, 1888) had published an extremely important monograph on the British "oribatid" (Cryptostigmatid) mites, which laid the foundation for the study of these typical and abundant soil- and litter-inhabiting creatures.

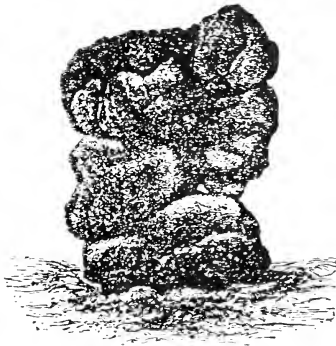
Towards the close of the 19th Century we should refer to further work on economically important root-feeding nematodes, for instance, the description of the root-knot eelworm of coffee *Meloidogyne exigua* by Goeldi (1887) in Brazil, and a fine monograph on the Sugar-beet eelworm, *Heterodera schachtii*, by Strubell (1888). One of the earliest workers to realize the important role of the fauna in comminution of litter and in humus formation was Keller (1887). Another was Kostýchev (1889), who recognized that passage of organic matter through the bodies of invertebrates (earthworms, millipedes, sciariid fly maggots), even if little chemical change occurred, was important, the excrement being more readily broken down by fungi. Related to this, though scarcely realized at the time, were the studies on the biology of



Tower-like casting from near Nice, constructed of earth, voided probably by a species of *Perichaeta* : of natural size, copied from a photograph.



A tower-like casting, probably ejected by a species of *Perichaeta*, from the Botanic Garden, Calcutta : of natural size, engraved from a photograph.



A casting from the Nilgiri Mountains in South India ; of natural size, engraved from a photograph.

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Fig. 39. Famous illustrations of earthworm castings published by Charles Darwin (1881); from photographs by Dr. King, when keeper of the Botanic Gardens, Calcutta.

UNTERSUCHUNGEN
ÜBER DIE
BODENFAUNA IN DEN ALPEN

INAUGURAL-DISSERTATION
ZUR
ERLANGUNG DER PHILOSOPHISCHEN DOKTORWÜRDE,
VORGELEGT DER
HOHEN PHILOSOPHISCHEN FAKULTÄT DER UNIVERSITÄT ZÜRICH
(MATHEMATISCH-NATURWISSENSCHAFTLICHE SEKTION)
VON
KONRAD DIEM
AUS HERISAU, APPENZEL A.-RH.

BEGUTACHTET VON DEN HERREN PROF. DR. A. LANG
PROF. DR. K. KELLER

ST. GALLEN
ZOLLIKOFERSCHE BUCHDRUCKEREI
1903

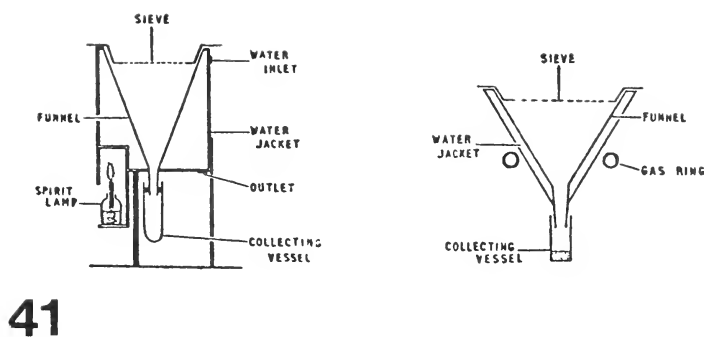


Fig. 41. Berlese funnels for extracting soil arthropods. Left, original pattern of Berlese (1905); right, early gas-operated modification. After Kevan (1962a).

millipedes by Rath (1890, 1891). Further investigations on the effects of earthworms on soil fertility were also carried out by Wollny (1890) and Djémil (1896), while various other earthworms studies were undertaken by Bretscher from 1895 until the end of the century, when he submitted for publication a paper on their biology, which appeared the following year (Bretscher, 1901).

1900 TO 1945

The 20th Century opened auspiciously from the point of view of soil zoology, for, under the direction of Professor Conrad Keller (see above), Konrad Diem undertook a comparative ecological study, from 1900 to 1902, of the animals inhabiting Swiss alpine soil and litter. In his doctoral dissertation (Fig. 40) for the University of Zürich (Diem, 1903), he briefly defined the term "*Bodenfauna*" (soil fauna) for the first time, and it would seem that his thesis was the very first attempt at an integrated faunistic investigation of soil and litter habitats anywhere. Though his methodology was quite unsophisticated, he considered not only the more conspicuous animals (earthworms, myriapods, gastropod molluscs), but also Collembola, nematodes and enchytraeids as best he could. Additional, less thoroughly treated groups were beetle larvae, fly larvae and "others". Mites seem to have been ignored. Indeed he admits to having difficulties with the smaller forms of life.

Another important step forward at about this time was the invention of the "Berlese funnel" for extracting mites and other small arthropods from soil and litter (Berlese, 1905). Berlese's name is still widely, but erroneously used for virtually all apparatus of a similar nature, but the original, water-jacketed funnel was heated, eventually by a gas-ring from *below* (Fig. 41), whereas all modern devices are unjacketed and heated (by an electric bulb or other device) from *above*. These are modified from the "Tullgren funnel" (Tullgren, 1917).

During the early years of the century, general interest in earthworms continued. Parker and Metcalf (1906) and Hurwitz (1910) were concerned with the reactions of these to salts and to acids respectively. Russell (1910) and Baugé (1912) again stressed the question of earthworms and soil fertility. Wieler (1914) also concerned himself with earthworms and soil reaction.

The publication by Russell (1912) of the first edition of *Soil Conditions and Plant Growth* "provided an enormous stimulus to the comprehensive study of the soil and its living organisms, but at that time not much could be included on the role of animals other than earthworms ..."

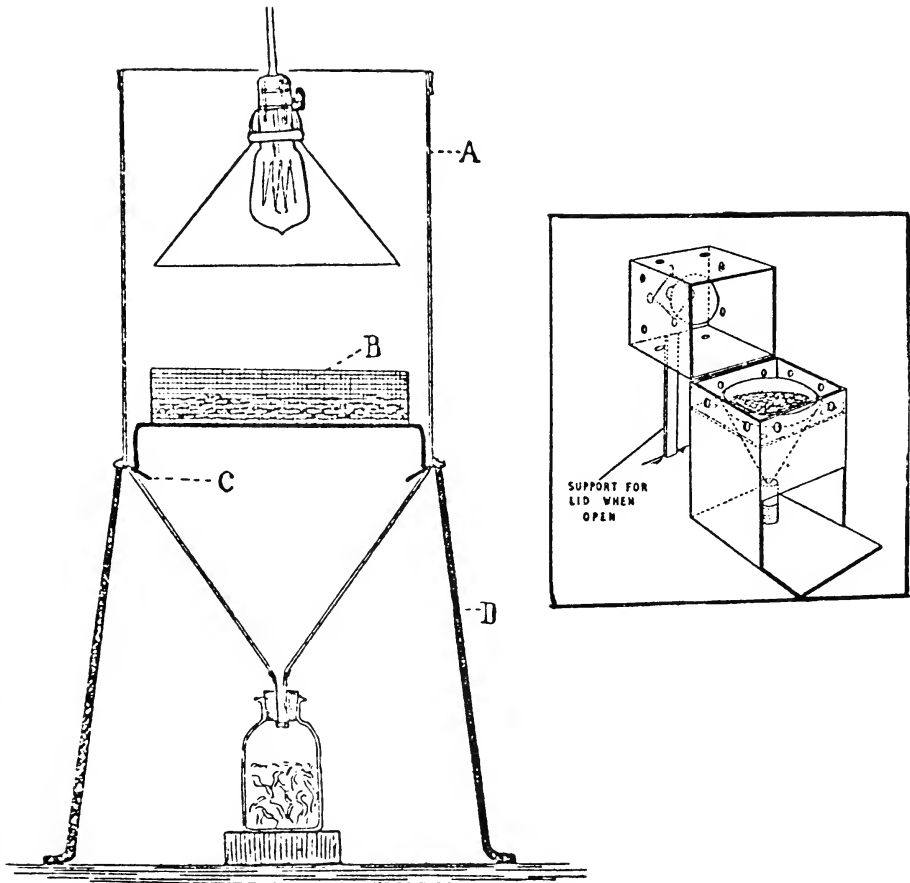
(Kevan, 1962a), and there was little enough of that. A sort of "two solitudes"³⁰ attitude on the part of self-styled soil scientists on the one hand, and of zoologists, on the other, seems to be traceable to this period. The former, for a long time, seldom paid attention to animals smaller than earthworms (which they ignored if they could), whilst the few zoologists who deigned to get their hands dirty were considerably retarded in their recognition of the pedological significance of the soil fauna. Most early studies by the latter had a direct or indirect bias towards crop pests, mostly insects or nematodes.

One of the earliest comprehensive studies of insects (and other arthropods) in the soil was that of Cameron (1913)³¹ in which the principal finding was that gravitational soil water was destructive, and capillary soil water favourable, to them. The paper was not concerned with effects of the fauna on the soil. On the other hand, Cobb (1915), in a pioneer paper attempting to popularize "nematology" (the word was introduced into the language here), suggested, though no basic information was available, that nematodes presumably bore an important relationship to the fertility and biology of the soil. (He was in error, however, in his opinion that the great majority of soil species possessed an oral "spear" and were injurious to plant roots). He estimated that, in an acre of North American alluvial soil, there may be 3,000 million nematodes in the top 3 inches (7.5cm). Cobb (1917, 1918) gives further estimates of nematode populations in sand and soil.

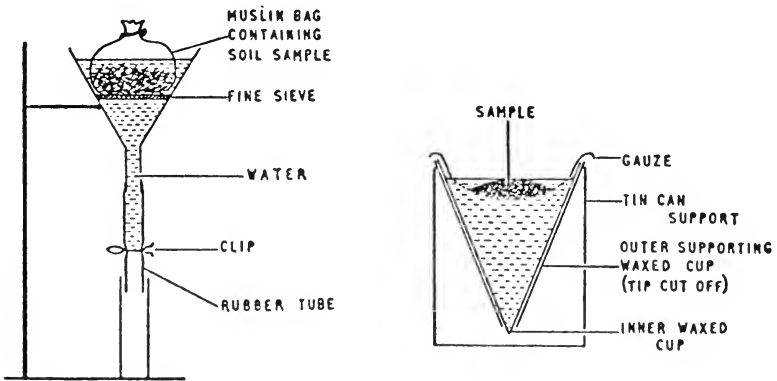
While the First World War restricted work on the soil fauna (as it did other endeavours) in most places, even in neutral countries, we may recall the appearance of Tullgren's (1917) funnel for extracting small arthropods (Fig. 42), and note the invention of another type of funnel for soil-inhabiting nematodes (Fig. 43), that of Baermann (1917). The latter was originally for retrieving the larvae of parasitic hook-worms from tropical soils, but it was subsequently used for nematodes generally, including those occurring in the faeces of vertebrates.

Probably the first Canadian contributions to integrated soil entomology were also published at this time, those of Cameron (1917a, b), though the larger of these related to work done previously in England. They stressed the importance of soil moisture and aeration, as well as of other factors, on soil insect ecology.

Over the next decade or so, no major stride forward was made in the study of the soil fauna, but we may mention a few publications of interest. Morris (1920) began his investigations on soil insects, reporting on their occurrence in permanent pastures; Jegen (1920) discussed the significance of enchytraeid worms in humus formation; Buckle (1921) investigated the fauna of arable land; Arrhenius (1921), Moore (1922) and Phillips (1923) were concerned with the effects of soil reaction (pH) on earthworms, whilst Salisbury (1923) looked at the question from the opposite viewpoint, the influence of earthworms on soil reaction and stratification; Micoletzky (1922) gave the fullest account to date of free-living soil nematodes; and McColloch and Hayes (1922) discussed the *reciprocal* relations between soils and insects. The year 1922 was also notable for the first serious attempt to use "wet" extraction methods for soil arthropods (Fig. 44), as introduced by Morris (1922a) for the purpose of his studies on these animals in arable land (Morris, 1922b, 1927). M. Thompson (1924) also undertook an extensive study on soil arthropods. Soil nematode investigation, especially on applied aspects also began to forge ahead. The distinctiveness and great importance of the Potato root eelworm (later called the Golden nematode in America) came to the fore, the name *Heterodera rostochiensis* being bestowed upon it by Wollenweber (1923); see papers by Wollenweber (1924) and Morgan (1925). Thorne (1927) investigated mononchid eelworms in arable soils in



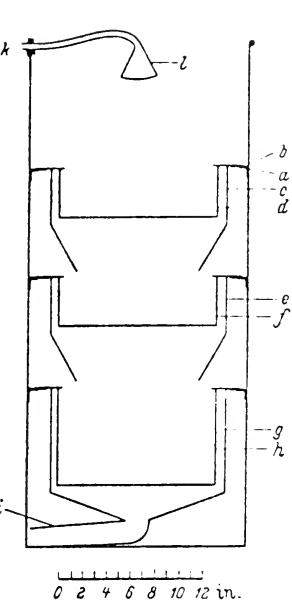
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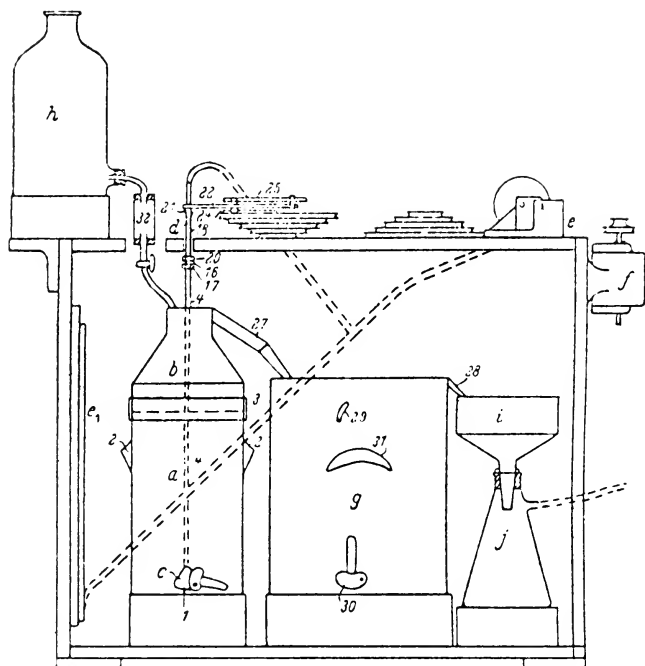
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Fig. 42. Tullgren funnels for extracting soil arthropods. Left, original design, after Tullgren (1917); inset, right, modified version of Haarlov (1947), after Kevan (1962a). Fig. 43. Baermann funnels for extracting soil nematodes. Left, basic pattern of Baermann (1917); right, Anderson and Yanagihara field pattern. After Kevan (1962a).

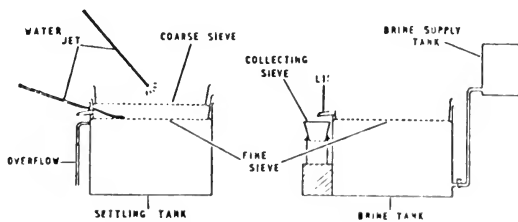
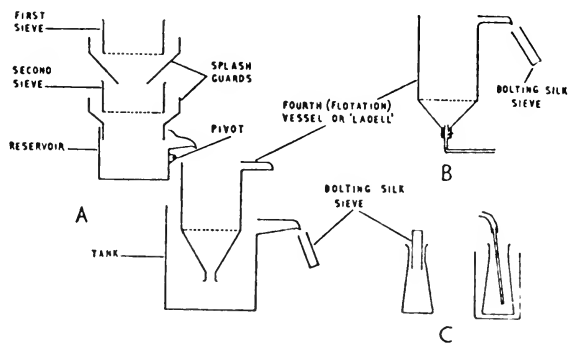
Fig. 44. Morris "wet" extraction apparatus for soil arthropods; after Morris (1922a). a, ledge; b, shelf; c, first funnel; d, first sieve with holes 3–5 mm in diameter; e, second funnel; f, second sieve, with holes 1–5 mm in diameter; g, third funnel; h, third sieve, with 50 meshes to the inch; i, outlet; k, inlet; l, rose. Fig. 45 Ladell flotation apparatus for extracting soil arthropods; after Ladell (1936). a, cylinder in which soil is mixed with liquid; b, conical head fitted to the top of the cylinder, with a watertight connexion; c, combined stirrer and air bubbler supporting two sieves; d, stirring mechanism; e, air pump; e₁, manometer; f, small electric motor for stirring; g, soil sedimentation tank; h, glass reservoir containing the solution; i, Büchner funnel; j, filter flasks; l, discharge outlet of cylinder; 2, handles; 3, rubber ring; 4, central tube of hollow stirrer; 5, hexagonal box of stirrer; 6, air tubes; 7, air outlet; 16, threaded collar; 17, hexagonal nut; 18, brass tube connexion; 19, flanged tube; 20, hexagonal back nut; 21, brass boss; 22, iron strap; 24, crank; 25, connecting arm; 27, chute; 28, lip; 29, overflow pipe; 30, discharge outlet of tank; 31, handles; 32, tap funnel. Fig. 46. Flotation apparatus for extracting soil arthropods. Above, Salt and Hollick (1944) apparatus (A, sieving; B, actual flotation; C, separation of arthropods from vegetation). Below, large-scale tanks of Cockbill *et al.* (1945). Both after Kevan (1962a).



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the United States, and Cobb (1927) summarized what was known about "nemas" (nematodes other than parasites of vertebrates) in general. Even in China these animals were receiving attention in soil (H.D. Brown, 1929). An important paper was published by Handschin (1926) on the Collembola of subterranean communities. Oudemans (1926, 1929) published the first two parts of his historical bibliography of mites. A little-known, annotated bibliography of cryptostigmatid or "moss" mites by Jacot (1929) should also be mentioned, and, so as not to forget earthworms, we should note an important contribution by Stöckli (1929) on the significance of these in soil formation.

In concluding our brief review of the 1920's, we should also refer to the comprehensive study of insects and other invertebrates in the soils of pasture and arable land by Edwards (1929), and to a characteristically American contribution to soil entomology – a machine (albeit still hand-operated) to facilitate the rapid recovery of insect larvae (specifically elaterid wireworms) from the earth (Lane and Shirck, 1928). Power-driven apparatus of increasing complexity was introduced later, but this will not be considered further here (for references, see Lang, Akesson and Carlson in Kevan, 1955: 351–355).

The beginning of the next decade was notable for the appearance of one of the classics of soil zoology, *The Fauna of Forest Soils*, by C.H. Bornebusch (1930), which had a very great impact on the study of the role of animals in forest soil ecology. In the same year, too, Mail (1930) stimulated interest in the effect of low (winter) temperatures on the survival of soil insects. Driedax (1931) published further investigations on the significance of earthworms for plant growth, and, in the same year, Nazarovff (1931) advanced the interesting theory, later generally accepted (Machado, 1983b), that large masses of spongy brown ironstone in lateritic areas of the African (and other) tropics were a result of "the ferruginization of termitaria". Ulrich (1933) made a notable quantitative comparison of the macrofauna of forest litter between good and poor stands of trees. Kollmansperger (1934) included extensive ecological information in his thesis on German earthworms; and Rommell (1935) gave a positive example of the role of myriapods in mull formation.

It was about this time that Jacot (1935, 1936), first in a short, popular article and then by a scientific paper, began his eloquent, but not very successful, attempts to interest North American biologists and/or pedologists in the fauna of soil and litter (especially of forest and woodland) for its own sake and from a pedological viewpoint.

Frenzel's (1936) monograph on invertebrates of all groups in meadow soils was the next large work in the field after that of Bornebusch. It appeared in the same year as Ladell (1936) proposed a new, rather complicated type of flotation apparatus for recovering insects and other arthropods (Fig. 45). In the following year, Ford (1937) published an important ecological paper on population fluctuation in Collembola and mites. A significant Canadian contribution on populations of soil insects was that of K.M. King (1939). Jacot's (1939) discovery that phthiracarid mites hollow out conifer needles without apparent external change in their form was also significant. Jacot (1940) also produced a very commendable, comprehensive review of animals in soil and litter, but again he seemed unable to influence American biologists or pedologists to any appreciable extent.

As the Second World War progressed, the need for food production focussed attention on the soil (except for large areas where this was being fought over). Even papers like that of Joachim and Kandiah (1940), comparing soils derived from termite mounds with those of adjacent land, took on added significance, as did Adamson's (1943) review of termites and soil fertility. Even the mole (*Talpa europaea*) and its relationship with earthworms and other soil

invertebrates received its share of attention (MacDougall, 1942). From a pedological viewpoint, the microscopic investigations of humus by Kubiěna (1943) showed the abundance and importance of the excrement of soil invertebrates for further decomposition of soil organic matter, Gisin (1943), in neutral Switzerland, published the results of an extensive study of the ecology of Collembola, and Starling (1944), in the eastern United States, studied the ecology of pauropods, a little-known group that proved to be much more abundant in the soil than had generally been believed. In England, however, intensive wartime studies of crop pests had been in progress, particularly on wireworms (elaterid beetle larvae) which were of special importance in crop fields that had previously remained unploughed for long periods. From these studies came, not only ecological information aimed at pest control, but the well-known flotation soil-extraction technique of Salt and Hollick (1944) and the large-scale flotation tanks of Cockbill *et al.* (1945) - see Fig. 46. And, of course, there was no lack of interest in earthworms and soil fertility. This even stimulated the reissue of Darwin's (1881) book on the subject, with a foreword by Sir Albert Howard, in which the latter expressed strongly his opinions against the use of "artificial" fertilizers.

Meantime, in neutral Sweden, extensive studies on the fauna of forest soil and litter had been undertaken for some time. These resulted, near the end of the war, in another large "land-mark" publication in the annals of soil zoology (Forsslund, 1945).

THE POST-WAR PERIOD TO THE 1960'S

Immediately after the war there was a gradual, then a rapid, expansion of work in soil zoology, although the subject had, as yet, by no means developed into a discipline like fresh-water biology. Pearse (1946) in the United States, Fenton (1947) in the United Kingdom, and Gilyarov (1947) in the Soviet Union, produced important contributions on forest soil faunas. Salt *et al.* (1948) continued with studies on pasture soils.

There was also considerable renewed interest in earthworms and their reciprocal relationships with soil conditions (Evans and Guild, 1947, 1948; Evans, 1948; Guild, 1948; Dawson, 1948; Dutt, 1948). Scandinavia, where soil fauna studies had always been pursued with vigour, continued to produce impressive results. Haarlöv (1947) modified the Tullgren funnel so as to increase its efficiency (Fig. 42, inset); his was the basis of numerous subsequent modifications, improvements and adaptations. Weis-Fogh (1948) related distribution of Collembola and mites within the soil profile to pore-space, using an elegant, new technique. Overgaard-Nielsen (1948) introduced new methods for nematode and rotifer extraction, and Forsslund (1948) recorded unprecedented numbers of arthropods from forest soils.

The same year also saw the publication of Kubiěna's (1948) influential *Entwicklungslehre des Bodens*. Although this was not the first time that this author had drawn the attention of other pedologists to the importance of small arthropods in humus formation, nor was it to be the last, it may be said that it was now, more than at any time previously, that "soil scientists" were made to sit up and take notice of soil and litter fauna, other than earthworms, in the process of soil formation.

The next few years saw the burgeoning of major works on the soil fauna. In addition to those in more restricted fields, like that on the soil nematodes by Overgaard-Nielsen (1949), they included books covering a wide field: Gilyarov's (1949) *Osobennosti Pochvy ... v Evolyutsii Nasekomykh*, dealing with the soil as a milieu for insect evolution; Franz's (1950) *Bodenzoologie ...*, largely relating to the importance of soil fauna for cultivation; Kühnelt's



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Second Easter School in Agricultural Science

SYMPOSIUM and
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on
SOIL ZOOLOGY

at

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Sutton Bonington, near Loughborough, Leicestershire,
England.*

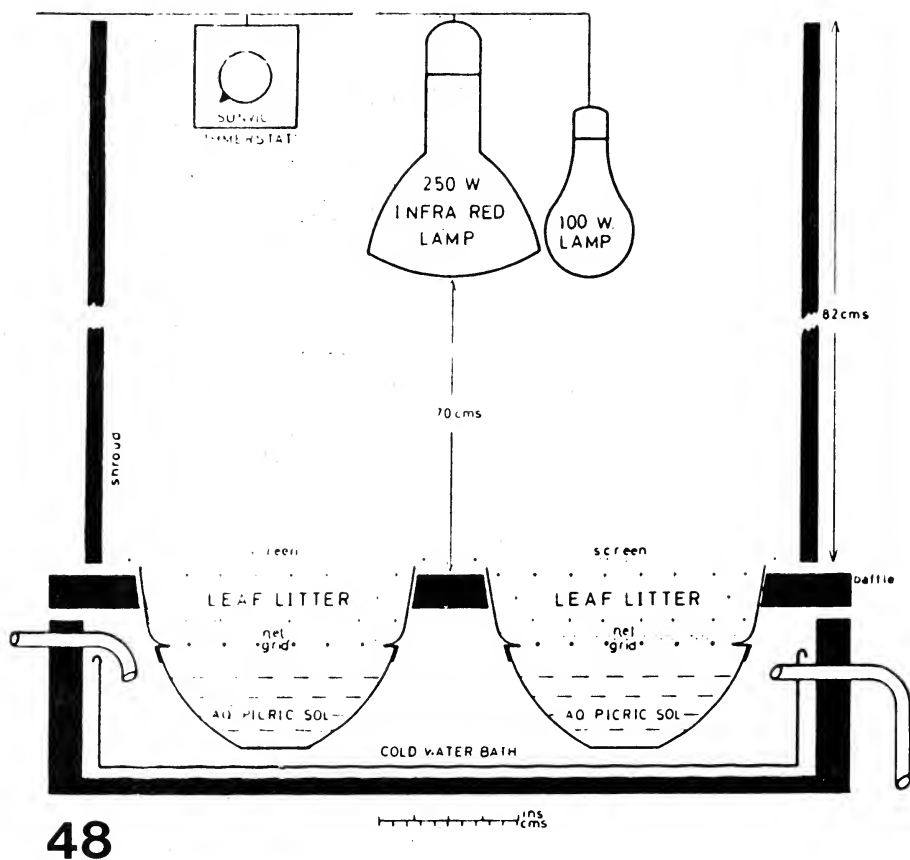
APRIL 1st to 7th, 1955 (inclusive).

(1950) *Bodenbiologie* ..., a general text on the soil fauna, later translated into Spanish and English, and Delamare Deboutteville's (1951) *Microfaune du Sol* ... with an emphasis on tropical as well as temperate conditions and taking into account soil formed above ground level on trees. At this time too, there appeared another large research report on the (mainly arthropod) fauna of temperate (beech) forest soil, which was to become a classic (Drift, 1951). Then Hartmann (1951, 1952) stressed the importance of soil fauna in his books on forest soil ecology. Soon afterwards came another important book, mostly relating to soil and litter fauna, but one which is not widely known to soil zoologists, and even less to pedologists, partly because of its title, *The Biology of the Cryptic Fauna of Forests* (Lawrence, 1953), and partly because it relates mainly to southern Africa. Also regionally restricted was *Fauna Pochv Latviškoj SSR* (on the soil fauna of Latvia) by Eglitis (1954). Although it would seem invidious to try to select any papers from the scientific journals, for particular mention, the valuable review by Birch and Clark (1953) should perhaps be excepted.

Pedological works, such as those of Kubišna (1953), Handley (1954) and Wilde (1954), now referred more and more to the importance of the soil fauna in humus formation, but it was the year 1955 that saw Soil Zoology finally emerge as a discipline on its own. In the previous year, almost exactly 30 years before this present meeting, I undertook, at the instigation of Professor E.G. Hallsworth, to organize the first³² international colloquium in the field, to take place from the 1st to the 7th April, 1955, at the University of Nottingham School of Agriculture, Sutton Bonington, near Loughborough, England (Fig. 47). The meeting - registration fee, then(!), 10 shillings (ca. \$2), accommodation - (all meals included!) £ 1.5.0 (ca. \$5) per diem! - was an unqualified success, bringing together scientists from many countries (though mainly European) and its proceedings (Kevan, 1955) published in record time, became "out-of-print" almost at once and are now very hard to obtain on the second-hand market. The Sixth International Congress of Soil Science, at its meeting the following year, fostered a greater interest than hitherto in the soil fauna, and there were several papers given in this field (International Society of Soil Science, 1956). This led to an ongoing series of international Soil Zoology colloquia, beginning in association with the 15th International Congress of Zoology in 1958 (International Congress of Soil Zoology, 1959; Murphy 1962) - see also Note 32.

From the time of the 1955 meeting onwards, too, soil animals also became emphasized in several major works on animal ecology, such as those of Tischler (1955), Macfadyen (1957, 1962) and Balogh (1958), in at least one introductory zoology textbook (Moment, 1958), and in some general books on soil, such as those of Russell (1957), though the United States Yearbook of Agriculture, *Soil* (Stefferdud, 1957), had very little space devoted to the subject, which was symptomatic of an unexpectedly retarded general interest in North America. Though both Canada and the United States had had in the past, and continued to have, their proponents of soil zoology (as distinct from those who worked with soil pests) they lagged far behind Europe, both western and eastern, in the field. Courses and research in Soil Zoology, as such, were, however, introduced by me into the McGill University (Macdonald College) programme in 1958-59, where they uniquely continue. Canadian perspectives of the times were also published (Kevan, 1959-61, 1962b).

In the late 1950's and in the 1960's, there was a very large increase in the number of publications on soil fauna in scientific periodicals. Of these, I will mention only a review by Kühnelt (1963), and a paper dealing with an important development in arthropod extraction technique by Kempson *et al.* (1963) - see Fig. 48. Significantly, however, many books and



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Fig. 48. Extraction apparatus for small soil and litter arthropods; after Kempson *et al.* (1963). Slightly modified versions of this type of equipment have resulted in the recovery of some of the highest recorded numbers of soil arthropods per unit volume.

monographs (other than taxonomic works, which we will not cover here) devoted, wholly or in large part, to the soil fauna appeared. Some of these were quite general, others restricted in their topics; some were large, some small; some placed an emphasis on humus formation, soil fertility etc., while others did not. They included: Paclt's (1956) book on the biology of apterygote Hexapoda, important soil animals; the Spanish and first English editions of *Bodenbiologie* (Kühnelt, 1957, 1961); a text by Nosek (1957); a "popular" book by Farb (1959); a research monograph by Haarløv (1960); Godfrey and Crocroft (1960) on the mole; *Principles of Nematology* by Thorne (1961); a book with an agricultural bias by Kipenvarlitz (1961); a general introductory text by Kevan (1962a), with an amended edition in 1968; a South American faunal series edited by Delamare Deboutteville and Rapoport (1962–68); texts by Schaller (1962, 1968) and Bachelier (1963), *The Physiology of Earthworms* by Laverack (1963); small "popular" works by Dunger (1964) and Palissa (1964); a localized account for the central Volga region by Aleĭnikova (1964); a voluminous tome on soil biology generally by G. Müller (1964); and, by contrast, a little booklet for amateurs by Moreau (1965); Gilyarov's (1964, 1965) monograph for the identification of soil insect larvae and handbook for diagnosing

soil types according to their fauna; a small highschool teaching manual by Pramer (1965), and a slightly more advanced introduction to soil life generally by Jackson and Raw (1966); a large monograph by Loksa (1966); a thesis with special reference to tropical Africa by Maldague (1967); a collection of specialist papers on various aspects of soil biology edited by Burges and Raw (1967); a text by Brauns (1968); and other works by Dunger (1968) and by Lamotte and Bourlière (1969), the last being of considerably wider significance than to purely soil ecology.

Meanwhile, further colloquia, symposia, etc., were being held in many places, internationally, nationally and locally. Some of the proceedings of these meetings were published as follows: Arnol'di *et al.* (1958), Murphy (1962), Dunger (1962), Klapp and Wurmbach (1962), Doeksen and Drift (1963), Rapoport (1966), Býžova *et al.* (1966), Minkevičius *et al.* (1966), Graff and Satchell (1967) and Aleinikova (1969). It is also interesting to note the widening interest in the soil fauna that was developing among non-zoologically oriented scientists. An address by P.W. Murphy to the Seventh International Congress of Soil Science at Madison, Wisconsin, 1960, on the role of animals in soil formation, was prepared for inclusion in one of the general sessions, though the text was never published (Kevan and Murphy, 1960; Kevan, 1961); Section II of a 1965 symposium on soil-borne plant pathogens began with an invitational address on soil fauna (Kevan, 1965); and the Ninth International Congress of Soil Science in Adelaide, 1968, opened one of its principal sessions with another such paper on soil fauna and humus formation (Kevan, 1968).

In this period, too, serial publications devoted very largely to research on soil fauna appeared. The first of these was merely an annual information bulletin (newsletter) resulting from a decision made at the Sixth International Congress of Soil Science (International Society of Soil Science, 1956). It was called *Microfaune du Sol* and began under the directorship of J. d'Aguillar in April, 1957. After the seventh number (in 1963) it was replaced by the larger and more comprehensive *Biologie du Sol*, beginning April, 1964, which eventually became *Pedofauna* in 1982 (nos. 35/36) under the direction of G. Wauthy. In the mean time, in 1961, Ekkehard von Törne, in Austria, had started the scientific journal *Pedobiologia*, and C. Delamare Deboutteville, in France, launched *Revue d'Ecologie et de la Biologie du Sol* in 1963. Both journals remained predominantly zoological for many years.

RECENT TIMES

During the past few years, there has been no slackening off of work on the soil fauna, and it would be quite impractical to try to review this here, even sketchily. Reference to abstracting journals and to the proceedings of congresses, etc., however, will show that the field continues to expand. One or two research publications for last year, taken at random, indicate that activity varies widely from basic preliminary surveys of the myriapod fauna of northern North America (Kevan, 1983, *c, d*) to the practical significance of the presence of heavy metals in the food of larger soil invertebrates (A. Carter, 1983)³³, both by Canadian authors, or as part of general biological studies of soils derived from loose sediments (Loub and Haybach, 1983).

Books and monographs on soil-zoological subjects since 1970 include that of Gilyarov (1970), to some extent a morphological development from his earlier book (Gilyarov, 1949); a little "popular" account for home consumption by Haarløv (1970); a specialized compilation edited by Delamare Deboutteville (1970); two soil-fauna ecology books by Wallwork (1970, 1976); a small "popular" book, more relevant to litter than soil proper, by Savory (1971); an International Biological Programme handbook on qualitative ecology edited by Phillipson

(1971); a collection of contributed papers edited by Pesson (1971); *Termites and Soils* by Lee and Wood (1971); *Biology of Earthworms* by Edwards and Lofty (1972); *Economic Nematology* edited by Webster (1972); an advanced high school-level ecological text edited by Andrews (1972) on soil organisms generally; a contribution to tundra ecology edited by Tikhomirov (1973); and introductory text for soil ecology by Richards (1974); *The Biology of Free-Living Nematodes* by Nicholas (1975); the enlarged new English edition of *Soil Biology (Bodenbiologie)* by Kühnelt *et al.* (1976); a text on soil invertebrates of the Soviet Far East by Kurcheva (1977); a small, general soil ecology handbook by A.L. Brown (1978); some account of the invertebrate fauna of brown and black soils in the Georgian Republic edited by Rekk (1979); *Nematodes in Soil Ecosystems* edited by Freckman (1982) - in which some of the contributions at last begin to consider the role of these animals in soil formation, as suggested by Cobb (1915); the Marshall *et al.* (1982) assessment of the (unsatisfactory) position of soil-faunal studies in Canada, which resulted in the present meetings; and Wallwork's (1983) little manual on earthworm biology. "Hot off the press", I may mention a review on micro arthropods and soil processes by Seastedt (1984) and a book on the distribution and ecology of Collembola (Gilyarov and Chernova, 1984) which has just reached me from the U.S.S.R. Also to appear shortly is a profusely (scanning-electron-microscope) illustrated work on European soil arthropods by Eisenbeis and Wichard (1985).

For this same period we should also mention various colloquium and symposium proceedings, including the following: Aguillar *et al.* (1971), Dindal (1973), Gilyarov (1973), Vaněk (1975), Górný (1975), Lohm and Persson (1977), C.A. Edwards and Veeresh (1978), Dindall (1980), Applehoff (1981), Veeresh (1981), Warden (1981), Satchell (1983), Lebrun *et al.* (1983), Grégoire-Wibo *et al.* (1983) and ("stop press!") Gilyarov (1984). It would also be appropriate to note an increased soil zoology content in works not primarily concerned with this; for example: in the 10th edition of *Soil Conditions and Plant Growth* (Russell and Russell, 1973); in *The Role of Arthropods in Forest Ecosystems* (Webb, 1977); in *The Encyclopedia of Soil Science* (Kevan and Hill, 1979); in *Recent Advances in Entomology in India* (Prabhoo, 1981); in *Soils, an Australian Viewpoint* (Greenslade and Greenslade, 1983); in *Laterization Processes* (Machado, 1983a, b); and in *Acarology VI* (Griffiths and Bowman, 1984).

CONCLUSION

In the foregoing I have included scarcely a reference to taxonomic literature, catalogues or nomenclators, which may surprise those who know me primarily as a taxonomist. This is partly because the subject is a vast one without definable boundaries, and partly because I hope that currently usable taxonomic related literature (from which one can often deduce the historical background) will be covered elsewhere at these meetings.

I would, however, stress that of all aspects of soil zoology, it is taxonomy that still needs the greatest *immediate* expenditure of effort which means *adequate financial support and increasing numbers of continuing positions for qualified research workers in taxonomy*. A dozen years ago I spoke of taxonomy as being the Cinderella of the sciences (Kevan, 1973) and I will not repeat what I said then. Since that time, however, the situation, at least in North America, has, if anything, deteriorated, and the attitude or understanding (or both) of non-taxonomists to the need for taxonomy has scarcely improved (see Note 33).

This does not mean that there has been no progress in the ability we now have to identify accurately the various members of the soil fauna. Indeed, there have been, particularly in

Europe (especially in the eastern countries), considerable advances, but even so, identification is often difficult there, too, especially in the case of some groups. In most of the world, including North America, any conscientious soil ecologist inevitably becomes bogged down by taxonomic problems. If he does not identify his animals properly, his research becomes greatly reduced in value, sometimes to the point of being worthless. On the other hand, without the means of identification (except in a few groups like Northern Hemisphere Collembola), what is he to do? The answer is, of course, "first things first; become a taxonomist!". Some have indeed followed this course, but the task-masters of most do not encourage it!

Soil zoology has come a long way from the days (mostly less than a century ago) when only a few, relatively conspicuous forms (I will not say "species" as identification was seldom so precise) were recognized, or even since the time of Gilbert White or Charles Darwin, when only an inkling of the importance of animals in the humification process was evident. We have reached all manner of degrees of sophistication in chemical, physical, statistical and electronic techniques, but we still know very little about the soil fauna itself. And our ignorance will persist until we can recognize one species of soil animal, in all its stages, from another, and learn about the biology of each one that is important, and in what way it is so. This, in itself, may not be immediately evident. Sometimes we may learn some answers, but mostly we do not! It does no good, for example, to lump all the mites or Collembola together, as is often done, for every species is different and each plays a different role. House sparrows are not usually lumped together with hawks, or even with other finches, nor is "humic" acid the same as formic and/or acetic! Yet this is the way in which "data" on the soil fauna have often been presented by otherwise competent "scientists"!

Even in recent times, with a few notable exceptions, there has been, to mutual disadvantage, a general scantiness of appreciation of the fauna on the part of "soil scientists" (how many of them have ever taken an appropriate course relating to soil zoology, though a few may have a smattering of microbiology?) and a reluctance to intrude into the realms of so-called "soil science" by zoologists (though a few agricultural and forest entomologists may have been exposed to an elementary course in "soil science" – without faunal content, of course!). There is still an almost complete lack of concern or comprehension, especially, it would seem, among those who determine (financially or otherwise) the directions of research, that we are still without the means of proper identification of innumerable members of the soil fauna. Furthermore there seems to be no realization that the understanding of basic soil ecology and thus of the pedological importance of the fauna is impossible without arduous, long-term taxonomic research and application, and that even "simple" identifications are very time-consuming. The competence *could* be created, but, even where some exists, it is seldom encouraged. Nay, it is discouraged! To admit to being involved in taxonomy seems to call for an apology - if not an admission of failure to accomplish anything worth while! The pundits would have others try to run before they have learnt to crawl, let alone to walk!

How far, then, have we really come since the Sumerians, or Aristotèles, or Albertus Magnus, or Darwin, or even Konrad Diem? A little way, perhaps, though, in some respects, not very far. We certainly know more species, but what do they do? As a result of these meetings, but not overnight, perhaps we shall take one more faltering step forward! Who knows what we might take two?

Our motto: "*Es wimmelt im Boden von Unbekanntem!*" (Gisin, 1947).

NOTES

1 The Akkadian for "ant" was given as *zirhabu*; the pale species (? termite) as *zirhabu šadi*; and the flying ant as *mutaprišu*. (Note, the Akkadians, unlike the Sumerians, did not seem to associate taxonomically the wingless with the winged ants; nor did they use a binominal system of nomenclature or seem to make much distinction between species; and their successors, in turn, were no more enlightened.) The Akkadian for (annelid) worm was *išqippu* or *išqapu*; for "mole cricket" (?) it was *hallalūa*, *hallalīa* or *hallullāa*; for "field cricket" it was *šaširu qīšte* or *šašari*; and for "dust locust" it was *erib turbuti*. One might also add a legless reptile to the soil-dwelling fauna known to the Sumerians. This was called *Muš* (generic for "serpent") *iginugal* or *Muš iginutug*; the Akkadians called it *puuḥmahu* or *upputum*. Scorpions (*gīr*; Akkadian *zuqaqipu*) were, of course, also well known, as might be expected, and several different kinds were distinguished.

2 Sandars' (1959) translation is entomologically a little confused, using "nymph" for "imago" and "larva" for "exuviae", but it is quite comprehensible. The Akkadian word for dragonfly from which her version is translated is *kulīlu(m)* and, for the nymph, *kirippu* (see also R.C. Thompson, 1928, who refers to both as kinds of birds!). For various Sumerian and Akkadian names for dragonflies, see Landsberger & Krumbiegel (1934). Gilgamesh, regrettably, does not refer to the soil fauna, unless one includes scorpions as such; a passage of some length relates to the "Scorpion-men". There is, however, a mention of honey and one of flies. Otherwise, invertebrates include only the prize, finally lost, of the "flower" of immortality at the bottom of the sea. This seems to have been based on a sea-urchin, rather than a sea-anemone, for the alleged aphrodisiac properties of the former have been claimed throughout the ages.

3 The *R̥gveda* (see Griffith, 1887) of ca. 1300 B.C.E. also makes reference to various kinds of "worms", for example in Book I, Hymn 191, and in Book II, Hymn 50, but these are to "poisonous" and parasitic species. The latter hymn is particularly interesting because it almost undoubtedly refers to two very important parasites of man, *Dracunculus medinensis* and *Wuchereria bancrofti*, neither of which, however, are soil-borne! The *Atharvaveda* (see Griffith, 1894), of a rather later date, ? ca. 1000 B.C.E., has more numerous references to "worms". A few involve plant injury, but most are concerned with flesh-consuming dipterous maggots in carrion or wounds, or with helminthic endoparasites (e.g., Book II, Hymns 31 and 32; III, 28; V, 23; VIII, 6; IX, 4; XI, 9). There is, however, in Book XII, Hymn 1, a single reference that just *might* refer to earthworms:

"The worm, O Prithivī, each thing that in the Rain revives and stirs ..."

4 The *New English Bible* translation of 1970, in Deuteronomy [II Moses] XXVIII, 42, however, uses "mole cricket" for the Hebrew *zelazal*, but this may be a mistranslation of an onomatopoeic word for a "whirring" (flying) locust of one kind or another (see Kevan, 1978: 197, 385, 467). Prof. I. Harpaz (*in litt.* 1985), however, suggests a true cricket, such as *Gryllus bimaculatus*.

5 Although of later date, it might also be appropriate here to mention the Jewish Talmud, which, like the Hebrew Scriptures, refers quite frequently to insects (Bodenheimer, 1928, 1929, 1960). Again there is virtually no unequivocal allusion to the soil fauna other than to ants, though Bodenheimer (1928) and Harpaz (1973) draw attention to the suggested biological control of these by transporting soil between (widely separated) nests in order to bring about mutual extermination by the inhabitants of each.

6 Hēródotos (see Rawlinson, 1910) did not refer directly to the amphisbaena, but, briefly only, to gaint Libyan serpents which were possibly part of the same tradition (though they may have been pythons from the south; the *draco* was the largest of all serpents and was a constrictor). The Arabian Flying serpents, about which he has much more to say, and which had featherless wings, ere clearly not soil-inhabiting amphisbaenas though, by Mediaeval times, the two seem to have become amalgamated (Fig. 7, 8 lower). Not only did the amphisbaena have two heads, but, by then, it seized one with the other and rolled along like a hoop! At the same time, it could also be Arabian and winged like the flying serpents of Hēródotos, and bipedal besides (*cf.* Druce, 1910; T.H. White, 1954; McCulloch, 1962; Rowland, 1973). It had illuminated eyes (in contrast to Nīkandros' description) and, in later Mediaeval times, some believed that its glance, like that of the bipedal Basilisk (discussed, for example, by the authors just mentioned), killed the beholder. An interesting feature of Hēródotos' flying serpents was that, at the precise time of fertilization, the female seized the male by the neck and would not let go until this had been bitten through. Surely the "flying serpents" were based on (elongate) praying mantids, though I do not recall having seen this theory advanced elsewhere. Furthermore, Hēródotos' concept, that the male gets his own back because the offspring devour the "womb" of the female, could be reconciled with the hatching of young mantids from the oötheca, regarded as a detached female abdomen! Thus the "classical" amphisbaena was originally based on a small, burrowing, legless reptile, but the late Mediaeval version may owe its "existence" in large measure to aerial mantids! The amphisbaena reverted to its true small form (only *seeming* to have a head at each end) in the 16th Century, though, even by the end of that century, Aldrovandi accepted the two-headed concept - see Druce (1910), who cites various classical and later authors in respect of it. There is a short precis of parts of Druce's paper in T.M. White (1954). Further

ancient beliefs that may be tied in with the mantis theory are discussed by Kevan (1985).

7 Although Latin versions of the *Physiologus* included less entries than the originals (the early 11th-Century metrical version of Bishop Theobaldus - see Rendell, 1928 - had but twelve, though the ant remained - Fig. 11), fabulous beasts multiplied in the later 12th- and 13th- Century "Bestiaries," as did their mythical qualities and their importance in symbolism, both religious and moral.

8 Later (705 A.D.) he became bishop of Sherborne. Aldhelm eventually went on to greater (posthumous) achievements, as he later became a saint of the Roman Church, a position attained by remarkably few (former) inhabitants of Great Britain!

9 Aldhelm also included riddles on the so-called "Bombix" or "silkworm" (perhaps not actually *Bombyx* itself, but some other cocoon-spinning caterpillar); *Apis* the honey-bee; *Locusta*, the locust; "*Scnifes*," the gadfly (*Tabanus*); "*Tippula*", the water-strider (*Gerris*), called "water-spider" by Pitman (1925); and "*Crabro*", the hornet (*Vespa crabro*). In addition, his riddle on "writing-tablets" mentions "honey-laden bees"; and he has another, rather unlikely invertebrate on his list, the "*Sanguisuga*" or medicinal leech (*Hirudo*). His riddle No. 18, "Myrmicoleon", with Pitman's (1925) English version, reads as follows:

*Dudum compositis ego nomen gesto figuris:
Ut leo, sic formica vocor sermone Pelasgo
Tropica nominibus signanspraesagia duplis,
Cum rostris avium nequeam resistere rostro.
Scrutetur sapiens, gemino cur nomine fungar!*

*I long have borne a name of hybrid form:
Both ant and lion I am called in Greek -
A double metaphor, foreboding doom:
My beak can not ward off the beaks of birds.
Let wise men search out why my names are twain.*

10 In 10th-Century Byzantine illuminated manuscripts, presumably copies from much older documents, there are representations of 8-legged, chelicerate (?) arthropods called "*myrmekion*" (see Kádár, 1978). These have been interpreted as ants (though they look more like tail-less arachnids -? pseudoscorpions much enlarged); perhaps they are supposed to be ant-lion larvae.

11 Sometimes called "Arabic" or "Islamic," but both these terms impose unwarranted restrictions of race, language and/or religion.

12 Born ca 1098, she became abbess of Disibodenberg (now Disenberg), in the diocese of Speyer, in 1136; she founded a new convent at Bingen in the Rupertsberg region, 1147, and died there 1179. She was famed for her visions, and prophecies and regarded as a saint, but she was never formally canonized by the Roman Church.

13 The "Bestiaries" became especially popular in England (and thereby the English part of France). The trend begun in the latter part of the 12th Century continued. Not only did fantasy increase, but so did the numbers of species mentioned, up to more than 100 (James, 1928; T.M. White, 1954, McCulloch, 1962). Among "soil" animals (other than this cricket) we begin to get further references (*cf.* Davis, 1958) to millipedes or woodlice (Fig. 13), as well as to earthworms, beetles, etc., only some of which had appeared earlier, not in the Latin versions of the *Physiologus*, but in Byzantine Greek copies of Nikandros and Diaskoridēs (Kádár, 1978). These additions, by further transcription, became carried forward into later centuries.

14 Neither referred to the amphisbaena. The works began to appear in various translations and, more than a century later, in printed editions. That of Bartholomew, being the most concise, was the most popular; it was printed in over 40 separate editions from 1470 onwards. The *Liber de Naturis Rerum* was often reproduced anonymously and usually attributed to Albertus Magnus. An early Flemish translation, written (between 1265 and 1269) in metrical rhyming couplets, was that by Jakob van Maerlant; it was called *Der Naturen Bloeme* (Bodenheimer, 1928). More notable, perhaps, was the German version by Cunrat (or Conrad) von Megenberg, called *Das Püch [= Buch] der Natur*, translated in the middle of the 14th Century. This eventually, became the first printed book devoted exclusively to natural history, complete with woodblock plates (Megenberg, 1475, Bodenheimer, 1928; Morge, 1973). One of these plates included illustrations of ants and earthworms underground.

15 The *Treatyse of Fysshynge* was added to the second printed edition of her(?) *Boke of Saint Albans*, published by Wynkyn de Worde, who changed the spelling of the lady's name. The first known printed edition of the *Boke* was that of

1486, printed at St. Albans by an unknown "Schoolmaster"; it did not include this *Treatyse*. The discrepancy between textual [1485(*sic*)] and bibliographic [1496] dates given by J.E. Satchell (*in* Dindal, 1980: 848) may thus be explained. [So far as I am aware, it is pure coincidence that two Satchells are involved here; the earthworm expert does not mention his namesake, whose publisher was another Satchell.]

16 Such religious and moral works on animals later included those like *Dierum Caniculatorum* by Simon Majolus, 1600 ([earth]worms, ants, "ant-lions," scarabaeoid beetles and cicadas mentioned), *Animalium Historia Sacra* by Wolfgang Franz, 1612 (a similar range of soil inhabitants, though omitting "ant-lions" and including crickets), and later, more famous *Hierozoikon* by Samuel Bochart(us), 1663 (also including references to a similar range of fauna) - see Bodenheimer (1928, 1929).

17 Georg Bauer (1494-1555) was from Saxony and was appointed physician to the German mining town of Joachimsthal in 1527. Thereafter he wrote many books on mining, metallurgy and chemistry. His interest in the subterranean fauna clearly stemmed from his interest in mines and diggings, not *vice versa*.

18 Here might also be an appropriate place to mention what appears to be a recently perpetrated fallacy regarding the 16th Century. In discussing the gall-forming nematode, *Anguina tritici*, which passes part of its life-history in the soil, and which causes what is known as ear-cockle of wheat, etc., Thorne (1961), as did others before him, suggested that the parasite was referred to by William Shakespeare, in *Love's Labours Lost* (Act I, Scene 4), when he wrote (about 1594, first performed ca. 1595, printed 1598), "Sowed cockle, reap'd no corn." It was not suggested that the causative organism was known (it was not discovered until 1743), but that infected seeds would not germinate. The *Oxford English Dictionary*, however, gives no earlier than 1836 as the first use of the word "cockle" in this context. The "Corn cockle" is in fact a caryophyllaceous weed, *Lychnis galigo*, though the name has also been misapplied to rye-grass (*Lolium*).

19 Also, although hated by farmers, careful attention was paid to mole crickets and their behaviour, for barley was seldom planted in spring before their chirping was heard. It was also noted that hoopoes (*Upupa epops*) eat mole crickets. This may possibly stem from the old Greek play *Ornithes* (*The Birds*) by Aristophanes, in which hoopoes are said to dominate over locusts or grasshoppers (see Kevan, 1978: 267-268), for these birds could scarcely be considered to be abundant in Central Europe. It is more likely, however, that the Lapwing plover or Peewit (*Vanellus cristatus*) was meant (*cf.* Yapp, 1984). It is further noted that the head of a mole cricket worn around the neck cures fever - again probably derived from an ancient source, for the wearing of a dead orthopteroid round the neck for this purpose is mentioned in a medical "jingle" by Joseph Ursinus, 1541, as quoted by Bodenheimer (1928: 218), as well as by myself elsewhere.

20 Browne (1646) also partially exploded the fable of the (soil associated) ant and the "grasshopper" by pointing out, firstly, that a cicada, not a grasshopper, was involved (the complexities of this are discussed by Kevan, 1978), and secondly, that the former insect lives for so short a time in summer that it need not "have recourse unto the providence of the Pismire [ant] in Winter." He was confused, however, as to what was a cicada, for these are virtually unknown in his native England, and he regarded the inhabitants of "cuckoo-spit" as such. As both are Homoptera, this was not unreasonable, though he said that from "cuckoo-spit ... some kind of Locust [*sic*] doth proceed." Had he paid a little more attention to Aristoteles' account of the life-history of cicadas, he should have known that they emerged from the soil. Later, Erasmus Darwin took Browne to task, but that is another story!

21 The only two-headed serpent indicated was the "*Serpens Biceps*", in which both heads were at the same end of the animal, and which was apparently treated as a mere freak, as it had been previously regarded.

22 See also Oudemans (1926), who gives a Dutch title and a date of 1664; the mites he identifies as "*Hypopus*" [now *Anoetus*] *feroniarum*; the nematodes ("*slangetjes*") he says were *Diplogaster* [now *Pristionchus*] *longicauda*; both identifications were presumptuous, though credible.

23 The second edition, of 1740, substituted *Fullo* for *Melolontha* and added to the species in "*Scarabaeus*"; the genus *Cicada* was added to the Hemiptera, from which *Scorpio* was removed to the Aptera; to the last was added the collembolan *Podura* (from Geer, 1740), and the terrestrial isopods in "*Oniscus*" became "*Millipes*". The 3rd edition, also of 1740, differed little in content from the 1st. The 4th edition, of 1744, resembled the 2nd, but additional groups were added, including Diptera and Hymenoptera, to the latter of which the ants were transferred. Subsequent editions (5th of 1747, 6th and 7th of 1748, 8th of 1753, from which botanical nomenclature dates, and 9th of 1756) gradually increased in scope, but added nothing significant for our purpose.

24 The rest of this volume was to have dealt with Coleoptera. Volume 8 was to have been on orthopteroids, etc., and volumes 9 and 10 on arachnids, myriapods and annelids (*cf.* Wheeler *in* Réaumur, 1926).

25 At the time, the condition was known as "malm"; the name "ear-cockle," according to the Oxford English Dictionary, did not appear (in print) until 1836.

26 Gilbert White's brother John included in the 1802 (posthumous) edition of "*Selborne*," various previously unpublished Ms. notes by Gilbert (together with remarks by William Markwick). These included further comments on earthworms as well as on ants, bugs, etc. Bingley (1803) plagiarized, almost verbatim, both original and supplement, though in dealing with mole crickets he cited White as his authority.

27 This was not done for more than a decade, when Schmidt (1871) published his studies on the pest.

28 Sir John William Lubbock, Baronet (later Lord Avebury), who lived at Down in Kent, near Charles Darwin, was a leading figure of the day, not only as a zoologist, Vice-President of the Royal Society and of the British Association, and Vice-Chancellor (administrative head) of the University of London, but also as a prominent banker and Member of Parliament. An even greater service than by his zoological writings that he rendered to mankind was to introduce the bill which established August Bank Holiday (known also to a select few as St. Lubbock's day!). His legacy lives on, even in parts of Canada, though his name scarcely does so! As he was so busy, it is often suggested that most of his writing was done for him by one or more "ghost" writers. This monograph, however, seems to have been entirely his own work (and he has signed himself "From the Author" in a copy I possess). The excellent plates are acknowledged as being the work of a Mr. Hollick, a deaf mute, and thus unique for the times.

29 Berlese's most active period in this field was from 1897–1900. From 1904–1921 he continued to publish on all groups of mites in *Redia*, 2–18.

30 I realize that this expression will not be familiar to all. *Two Solitudes* is the title of a well-known novel by McGill University author (John) Hugh MacLennan. The book, published 1945, deals with the isolation of the "French" and "English" cultures of Québec, and of Montréal in particular.

31 Alfred E. Cameron, a Scot, came to the Canadian Department of Agriculture from England about 1916 (he was not acceptable for the armed forces on account of his club foot). Later he became Professor of Zoology at the University of Saskatchewan. Later still he was Reader in Agricultural Zoology at the University of Edinburgh, and it was there, about 25 years after his paper was written, that, as an undergraduate, I first read it and another in the same vein (Cameron 1917a) - my first taste of soil zoology. I did *not* immediately engage in this field, but I take this opportunity to express my appreciation of what I owe to my late mentor.

32 It comes as a surprise to some to find that International Colloquia on Soil Zoology are now numbered as if they began with the one held three years later at Rothamsted in 1958 (International Congress of Zoology, 1959; Murphy, 1962). Thus the last one to be held in Louvain la-Neuve in 1982 (Lebrun *et al.*, 1983) was numbered "VIII", not "IX"! This is because the Biology commission of the International Society of Soil Science seemed to consider that they had a prerogative stemming from a decision made at their 1956 congress (Int. Soc. Soil Sci., 1956) at which, for the first time, the Society had paid more than scant attention to the matter. The numbering therefore applies only to colloquia sponsored by the Society. The intervening *International Colloquia* were as follows: II, Oosterbeek, Netherlands, 1962 (Doeksen and Drift, 1963); III, Braunschweig, West Germany, 1966 (Graff and Satchell, 1967); IV, Dijon, France, 1970 (Aguillar *et al.*, 1971); V, Praha, Czechoslovakia, 1973 (Vaněk, 1975); VI, Uppsala, Sweden, 1976 (Lohm and Persson, 1977); and VII, Syracuse, New York, U.S.A., 1979 (Dindal, 1980). Colloquium "IX" will be in Moskva, U.S.S.R., 1985. It may also be noted that the 1955 colloquium itself was likewise misnumbered, for it was called "The University of Nottingham Second Easter School in Agricultural Science," whereas it was really the *first* of its series. There had, indeed, been a not very widely publicised series of pedology seminars conducted in 1953 by guest-lecturer W.L. Kubiěna, but this was quite a small affair without published "proceedings". It may now be disclosed that it was dubbed the first "Easter School" only in retrospect, the better to promote the "second"!

33 Including some of the same myriapods (millipedes), which, like most of the other animals referred to are unidentified. This is typical of much work by "soil scientists" who emphasize "precision and accuracy of chemical analysis", but who do not even comment on the lack of this in the animal species investigated by them!

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SOIL MICROMORPHOLOGY AND SOIL FAUNA: PROBLEMS AND IMPORTANCE

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CANADA

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ABSTRACT

Surface soil layers were viewed microscopically along a pedogenic gradient from the northern Arctic to the southern Parklands within the Interior Plains region and westward to the Alpine and Interior Grasslands of British Columbia. In all instances it appears that soil animals play a major role in structural development although the relationship between humus form, synecology and microfabrics remains vague. Among all animals present microarthropod influences are the most ubiquitous in their influence upon soil microstructures and humus formation. Larger animals are more prominent in the Parkland region and appear to play a major role in regulating humus form; while moder humus form is most evident in the cold northern regions of the Arctic, proto-mull appears to be more characteristic of the warmer Parkland environment. Humus form of the Interior Grasslands is generally characterized by moder and little is evident for the action of larger soil animals upon development of soil microstructure; the reason for this is not clearly understood.

RÉSUMÉ

Les horizons supérieurs des sols ont été examinés au microscope le long d'un gradient pédogénique s'étendant du nord de l'Arctique jusqu'au Parklands des Plaines au sud et à l'ouest jusqu'aux Prairies alpines et des plateaux intérieurs de la Colombie-Britannique. Dans tous les cas, il semble que la faune du sol joue un rôle primordial dans le développement de l'aspect structural, même si les rapports entre la forme de l'humus, la microtexture et la synécologie sont encore vagues. De toute la faune du sol, les microarthropodes contribuent le plus à la microstructure des sols et à la formation de l'humus. Les éléments plus gros de la faune sont plus communs dans la région des Parklands et semblent y jouer un rôle primordial dans la détermination de la forme d'humus. La forme moder d'humus est plus répandue dans les régions froides de l'Arctique alors que le proto-mull semble caractériser davantage l'environnement plus chaud des Parklands. La forme d'humus des Prairies de l'intérieur est généralement caractérisée par du moder, et, pour des raisons que l'on s'explique encore mal, on y observe peu d'évidence indiquant l'action des éléments plus gros de la faune du sol sur le développement de la microstructure.

INTRODUCTION

The Problem

The principal problem facing those who work in micromorphology and formation of soil microstructure in relation to faunal activity, is the general lack of clarity as to the importance of soil animals in initiating and maintaining soil fabric rearrangement. Of secondary importance is the need for more precise cataloguing of a specific feature or features that each organism or group of organisms is capable of contributing to the reorganization of soil materials.

Early Research

The importance of soil animals in soil structural development has long been recognized. Contributions from earthworms have been singled out for special attention by early researchers such as Charles Darwin and P.E. Müller. Kubiena (1953) described forest mull as comprising earthworm casts and their residues and to this he attributed the 'crumb' structure that is so characteristic of these layers. However, as Jacks (1963) accurately pointed out, while it is generally accepted that earthworms create crumb structures of Russian Chernozems, these animals are not generally all that common in North American Prairie soils and crumb mull structures must be produced without earthworms.

Many previous researchers involved in this area of study were convinced other animals were also important contributors to soil reconstruction at the microscopic level (Kubíková and Rusek, 1976; Zachariae, 1963, 1964; Babel, 1973). They not only emphasized the ecological importance and soil genetic contributions of faunal associations but in some instances were able to assign unique fabric arrangements to manifestations of very specific biological activity. Even in his initial work Dr. Kubiena (1953) insisted upon a firm genetic role for soil organisms in reorganization of soil fabric.

Classification of Soil Microstructure and Faunal Activity

From 1938 to 1970 Dr. Kubiena published several textbooks and many scientific articles in which he clearly set forth his concepts on this subject. His fabric type most closely associated with faunal action was *spongy* microfabric. Spongy microfabrics were defined as consisting of aggregates bound to each other in a manner that forms a system of interconnected voids and cavities. The internal structure of the aggregates generally remains quite porous. Spongy microfabrics are most frequently associated with mull layers common to the A horizons of soils such as those of the Chernozemic and Brown Forest groups and were believed to be derived entirely through the activity of diverse faunal populations, especially earthworms and potworms. This type of fabric arrangement is regarded as superior to all others from an ecological and management standpoint. Kubiena (1938) also paid attention to forms of moder humus. However, because of the non-coherent nature of these materials their classification was considered at the *elementary fabric* level as some variation of the *agglomeratic* related distribution pattern. This approach is understandable since moder humus comprises a loose mixture of partially decomposed plant remains, mineral fragments and numerous droppings of small arthropods.

Kubiena's terminology for classification of biologically generated soil microfabrics provided a basis for further development by other workers. Up to the time of publication of his text on 'Fabric and Mineral Analysis of Soils' in 1964, Brewer had not given particular emphasis to faunal processes as a basis for classification, however, their influences upon the soil were recognized. Fecal pellets were described as a special kind of *pedological feature* and when deposited in a recognizable channel or chamber they comprised the inner material of some varieties of *pedotubules*. Unfilled *channels* and *chambers* have been attributed in some instances to the burrowing action of animals.

Barratt (1964) attempted to clarify some of the confusion that existed in the classification of humus types and humus forms. Subdivisions of forms of mull and mor humus were described micromorphologically. Class divisions were based on the manner in which organic matter was incorporated (material composition) as well as on the organization (arrangement) of material. Terminology for the initial classification reflected terms used for subdivisions of various humus

forms. Later Barratt introduced new terminology recognizing reorganization and composition of fine (-*col*) and coarse (-*skel*) materials. The terms *pelleted* and *spongy humical* and *mullicol* most frequently served to distinguish fabrics derived from discrete and welded casts from various soil animals, some of which are capable of intimately incorporating fine mineral components within the humus forms. Fecal pellets were recognized as an important component in all but raw humus forms.

Stoops and Jongerius (1975) also devised a classification based on spatial arrangement of fine and coarse materials. Aggregated materials such as fecal pellets were considered as discrete entities and divided into fine (*f*) or coarse (*c*) material depending upon size. Thus, fabrics comprising discrete fecal pellets all falling into one size group would be classified as *monic* while fecal pellets of finer size arranged in the intergranular spaces of coarse skeletal particles would be classified as *enaulic*. Kinds of materials were recognized by using suitable suffixes as for example recognizable plant fragments as *phyto*-, well decomposed humus as *humo*-, clay minerals as *argio*-, etc. As with Barratt's classification, unique kinds of fabrics could be assigned to activity of specific fauna or faunal groups.

Drawing on concepts by previous workers interested in fabrics of soil organic matter, Bal (1973) proposed that major emphasis be placed on the soil organic component in his concept of the *humon*. The *humon* is defined as "the collection of observable organic bodies in soil which are characterized by specific morphology and spatial arrangement." Excrement or *modexi* and comminuted plant material were considered to be important components of the *humon* and their specific morphological classification was based on size, shape, composition and distribution. Bal thus proposed a micromorphometric system for identification of fecal casts but one lacking emphasis on mode of origin. As Bal pointed out, characteristics of *modexi* are not always unique for a single animal species and knowledge of populations is also an essential element required for assignment of mode of origin. This is especially evident when aging of excrement has progressed to the point where individual *modexi* are no longer recognizable. In some instances the genetic origin of the fabric type may remain in doubt, since similar features may also be formed by non-biological processes. Biochemical substances (Martin, 1946), frost processes (Post and Dreibelbis, 1942; Fox, 1979) and wetting and drying (Russell, 1973) are examples of processes to which granulation of soil material has been attributed in the past. Formation of organo-clay complexes in mull layers has been attributed to biochemical processes active outside of, as well as within, the intestinal tracts of soil animals (Satchell, 1967).

A micromorphological Classification for Western Canadian Soils

Recent investigations of western Canadian soils developed under grassland, tundra and alpine plant communities with a significant component of grass, forbs and shrub species revealed A horizons with strong granulation at the macro and/or micro levels of fabric reorganization. These soils are in various Soil Orders in the 'Canadian System of Soil Classification' but all have well developed Ah horizons. In order to accommodate these fabric arrangements into a suitable micromorphological classification system, Brewer and Pawluk (1975) further developed a scheme published by Stoops and Jongerius (1975) that recognized special related distribution patterns between fine (*f-matrix*) and coarse (*f-member*) material. Brewer (1979) later introduced the concept of *fabric sequences* which allowed grouping of *fabric types* that exhibited unique genetic relationships. In this regard the fabric sequence that best accommodates the granular character of our soils is the *granic* sequence. The granic

sequence comprises four fabric types: *granic*, *granoidic*, *granoidic porphyric*, and *porphyric*. The granic fabric type is used for microstructures comprising units that are discrete and unaccommodated. Such an arrangement is commonly associated with discrete fecal pellets. Granic units of fabric partially coalesced or fused at their edges are referred to as granoidic fabric type (Kubiena's spongy fabric). Granoidic fabric types commonly grade to porphyric types i.e. coalesced units become more densely packed, individual units are no longer recognizable and form a vughy or porous groundmass of coherent soil material. Composition of encompassing material is defined through the use of appropriate prefixes: *humi* - well decomposed humus; *mull* - organo-clay complexes of the mull humus form; *phyto* - partially decomposed plant remains; *ortho* - mineral grains; *matri* - soil matrix constituents (largely inorganic). A mull with spongy fabric is thus designated as mullgranoidic fabric type. Since surface soil horizons of many of our most agriculturally productive soils show mixed granular microstructures with a variable degree of coalescence, the granic sequence is an especially useful concept for descriptive purposes and is used throughout the remainder of this discussion.

Objectives

Surface layers of soils, when viewed microscopically along a pedogenic gradient from the northern Arctic to the southern Parklands within the Interior Plains region and westward to the Alpine and Interior Grasslands of British Columbia, reveal interesting ecological and micromorphological relationships. In all samples it appears that soil animals play a major role in structuring and regulating soil microfabric development. Yet, the relationship that exists between humus form, synecology and microfabrics is poorly understood. While no attempt can be made here to fully develop a meaningful understanding of the dynamics, micromorphological features will be presented in an attempt to illustrate some of the resulting features within the soil fabrics and problems related to discerning their genesis will be raised.

OBSERVATIONS ON SOIL MICROSTRUCTURES FOR SURFACE SOIL LAYERS FROM DIFFERENT BIOCLIMATIC REGIONS

Northern Tundra Region (Table 1.1)

Surface soils examined from the ridge area on Devon Island showed comminuted plant material associated with mineral grains and fine (20-50 μm) humigranic units in a granic fabric arrangement. The humigranic units were relatively uniform in size but somewhat irregular in shape. Some were fecal pellets of microarthropods most likely Collembola and some were melanized plant fragments and cellular tissue. Numerous loosely bound fecal pellets of 200 μm size and comprised of smaller fecal pellets, melanized plant materials and silt size skeleton grains were similar to those reported in the literature for Enchytraeidae. Plant material appeared to be darker and more strongly humified in these latter fecal pellets. The composition is an expression of the feeding habit of the larger fauna. Uniformity in size and shape of fecal pellets reflects the limited diversity in faunal population of these soils. The lack of clay mineral constituents in the fecal material at least in part results from the low content in the soil.

Southern Tundra Region (Table 1.2)

Three well drained soils were studied in the southern Tundra region. Humus forms were essentially similar at all three sites. The moder humus form was well developed and comprised a dominance of humified comminuted plant fragments and fecal pellets from various fauna.

The majority of fecal pellets were of 30-50 μm size, irregular in shape and made up of amorphous humic materials. These were believed to be the droppings of Collembola. Larger humic fecal pellets of 200 μm size in the upper layer frequently contained loosely bound fecal pellets of smaller size as well as humified plant fragments. Similar fecal pellets reported in the literature (Kubíková and Rusek, 1976) were considered to be droppings of Enchytraeidae. Well developed humic fecal pellets of 350-600 μm size resembled droppings of Diplopoda. In some instances the larger fecal pellets were either disintegrating or were being destroyed by microarthropods that left their droppings in the voids. Mull-like fecal pellets of 350-400 μm size formed a thin horizontal zone in the lower moder layer. These fecal pellets were generally smooth, lobate and dense, closely resembling those of Diplopoda. The occasional large humus fecal pellets (900 μm) in this zone were similar to those of Diptera larvae or earthworms. Alignment of unassociated coarse mineral fragments suggested incorporation into the humus layer by frost action.

The immediate underlying soil layer appeared to be a 'proto' mull or mull-like moder. Some smaller mullgranic units of 50-90 μm size strongly resembled Collembola fecal pellets although others appeared smoother and more rounded. Fecal pellets of Enchytraeidae were also very common in this layer. Strong coalescence made it difficult to discern the original nature of most units. Units in the underlying layer became much larger and made up of loosely packed mullgranic material 450-500 μm in size with smaller units of 40-200 μm size in the voids. The smaller units were fecal pellets of Collembola and Enchytraeidae. Origin of the larger units was difficult to discern. In some cases smaller fecal pellets were observed within the larger units. This probably reflects microarthropods feeding on the larger units. The well-rounded moderately accommodated weak mull-like granoidic units in the A(B) were relatively large (1-2 mm) and their origin is unknown. The relatively high amounts of amorphous material found in the fine fraction suggests possible binding associated with freeze-thaw processes.

Forest-Tundra Transition Region (Table 1.3)

The raw soil humus of the lower leaf mat contained a high percentage of partially decomposed comminuted plant fragments together with small (50-90 μm) cylindrical humic fecal pellets most likely of Collembola. There were zones in which the larger fecal pellets (120-200 μm) of Enchytraeidae were concentrated. The underlying forms of moder humus contained an abundance of humic fecal pellets of 50-200 μm size that probably at least in part reflected the activity of Collembola and to a greater extent Enchytraeidae. Lesser amounts of partially decomposed comminuted plant fragments as well as occasional large (850 μm) fecal pellets likely of Diptera larvae were also evident. Humus fecal pellets of 400-600 μm size, that were smooth and usually quite dense, were probably casts of Diplopoda. The Ah horizon had a mull-like fabric arrangement comprised of coalesced fecal pellets dominantly 50-90 μm size and somewhat lesser amounts of units 180-240 μm in size. The units were usually relatively compact mull-like material, smooth in form and frequently lobate or round. However, some units had characteristics of fecal pellets of Collembola and Enchytraeidae (Rusek, 1974) and they were the most likely contributors to this fabric type. Occasional larger units present (350-600 μm) were probably fecal pellets of Diplopoda. Fecal pellets of Collembola were also observed in aggotubules.

Boreal Forest Region (Table 1.4)

The form of upper moder humus within the organic layer comprised partially decomposed plant fragments and fecal pellets of variable size. Fecal pellets (25 μm) of Acari were associated with decomposing plant fragments. Most fecal pellets were relatively uniform, fairly smooth in outline and of 90-125 μm size. There were also zones of units 50-60 μm in size. The variation in size distribution between zones of fabric may reflect the presence of different species of Collembola. Relatively few irregular shaped, loosely structured units of 125-250 μm size probably were Enchytraeidae droppings while larger units of 600-750 μm size were likely produced by Diptera larvae or small earthworms. Rare large earthworm casts (1.8 mm) were found at the mineral surface contact. Fungal hyphae were abundant throughout the humus layer. This layer showed sharp demarcation from the underlying mineral soil. Mixing of organic and mineral material is minimal and likely reflects the general lack of larger fauna in the population.

Transition Aspen Parkland Boreal Forest Region (Table 1.5)

Forms of moder humus contained an abundance of fecal pellets of highly variable size and shape ranging from 35 to 950 μm in size as well as variable admixtures of partly decomposed plant fragments and few mineral grain f-members. Humic fecal pellets, irregular in shape and of 30-50 μm size, dominated, probably reflecting the presence of Collembola. Many well rounded and lobate units of similar size were likely droppings of Acari. There were zones of concentration of smooth round fecal pellets of 90-125 μm size that strongly resembled major units believed to be dropping of other species of Collembola in many of the northern soils. Other animal origin cannot be discounted, for example because of their similarity to droppings reported for Isopoda (Kubíkoř and Rusek, 1976). There was a significant volume of smooth, loosely bound fecal pellets of 350-600 μm size that comprised both humus and mull in the upper layer and mull in the lower layer. These appear to be droppings of Diplopoda. A few large (940 μm) fecal pellets of Diptera and/or small earthworms were also present. The lower H layer was made up of partially coalesced fecal pellets dominantly 25 to 40 μm in size but also contained a significant amount of fecal material in the 120 to 180 μm size range. A lesser amount of fecal material 400-600 μm in size was also present. Most fecal material showed evidence of breakdown that probably reflected aging of collected fecal casts from animals similar to that active in the upper layer. The 'zone of mixing' that intergrades to the Ah had a greater dominance of mull fecal pellets of 200-550 μm size typical of that for Diplopoda. Fine mull fecal pellets of 90-125 μm size, very similar in structure to the humic units of the H layer were also evident.

The Ah layer had greater dominance of larger fecal pellets of 600-750 μm size. In most samples these fecal pellets comprised closely packed smaller units of 45 μm size some of which were made up entirely of humus and others of mull-like material. However a minor portion of the larger units frequently contained mineral matrix material brought up from the lower solum. These fecal pellets closely resembled those of Diplopoda and it appears that they may have played a very significant role in mixing organic and mineral materials in these soils. Large earthworm fecal pellets were relatively rare, however small earthworm casts maybe confused with those attributed to Diplopoda. Observed banded fabric reflects freeze-thaw processes but whether these same processes contribute to formation of well developed microstructural units is as yet uncertain.

Prairie Parkland Region (Table 1.6)

Humigranic and mullgranic units within fabrics of the Ah horizon were largely fecal pellets varying in size from 30 μm to 2 mm. Most of the finer (30-45 μm) fecal pellets probably reflected the presence of Acari and Collembola. Largely humic in composition, they were concentrated in the upper zones of the horizon. Some humigranic units were also melanized plant fragments. The larger mullgranic units (350-750 μm) were diverse in size and degree of compaction and probably reflected the presence of a wide variety of fauna including Diplopoda, Enchytraeidae, Isopoda, small earthworms and Diptera larvae. Contributions from large earthworms (1-2 mm) were much less common and frequently consisted of matrix material from underlying horizons. While the humus form was generally mull-like, the presence of diverse, discrete, poorly homogenized units of soil material suggests an immature or 'proto' stage of mull development.

Alpine Region (Table 1.7)

Humigranic units in the moder layer appeared to be largely fecal pellets of Enchytraeidae and microarthropods with a significant component of melanized comminuted plant fragments. Very few large fecal pellets (450-550 μm), likely those of Diplopoda, were evident as well. The Ah showed an increase in dominance of weak mull units of 20-400 μm size that at least in part reflected the activity of Collembola, Acari, and Enchytraeidae. Diplopoda were likely responsible for the very rare large fecal pellets of 600 μm size. Well rounded compact fecal pellets of 90-125 μm size were commonly present. While their origin is doubtful these casts may be formed by specific species of Collembola. Biological influence at depth was more difficult to discern because of the presence of orthogranic units of similar structure that reflected the presence of amorphous constituents such as perlite and volcanic glass. The lack of well developed mull probably reflects the low clay content.

Intermontane Prairie Region (Table 1.8)

The mull-like moder Ah comprised at least in part an abundance of fecal pellets of microarthropods (35 μm), few Enchytraeidae (90-200 μm) and very few Diplopoda (450-600 μm). As with most other soils dense, smooth droppings of 90-125 μm size were commonly present. All fecal material appeared humic in composition under low magnification. Plant fragments frequently had Acari fecal pellets within their decomposing structure. Frequently mineral grains were observed to have organic cutans that probably resulted from deposition of relatively mobile humic substances by wetting and drying and/or freezing and thawing processes. Clay content was low and relatively ineffective in stabilizing humic material.

CONCLUSIONS

All soils from the Northern Tundra to the Parkland regions had microfabrics of humus-rich layers that were considerably modified through faunal activity. The animals acted in several ways. They were responsible for comminution of plant fragments and reorganization of humic and fine mineral material into discrete microstructural units. In some instances their ingestion appeared to enhance mull fabric development through formation of organo-clay complexes. Their channels modified soil porosity and often remained filled with fecal material as pedotubules.

Among all the fauna present microarthropods appeared to be most ubiquitous in their influences upon soil microstructures. Fecal pellets of Acari were usually associated with partially decomposed plant fragments but those of Collembola appeared to be more broadly distributed and of much greater abundance. Fecal pellets of Collembola were found at all sites and dominated in the moder humus forms of the northern Tundra region and Intermontane prairie. In mineral soils collembolan fecal pellets usually occupied voids or old root channels and consisted of enclosing soil material which may have been humus, mull or mineral matrix varying with the niche they occupied. Enchytraeidae were also widely distributed geographically and not all of their fecal pellets were distinguishable from those of Collembola (Hale, 1967). They contributed significantly to fabrics of Alpine, Parkland and Forest-Parkland transition regions. Along with fecal pellets of other larger animals such as Diplopoda and larvae, Enchytraeidae also contributed significantly to the formation of mull fabrics found in the upper soil layers. Earthworms did not appear to play as dominant a role in mull formation in these soils as they do elsewhere (Kubiena, 1953), even though small earthworms are plentiful in some Parkland soils. In some samples it is difficult to distinguish between casts of small earthworms and Diplopoda. Fecal pellets of Collembola and larger animals incorporated organic and mineral constituents that vary in dominance with the degree of soil mixing. Fecal pellets were observed to comprise pure humus, pure mineral matrix as well as mull at different stages of formation. No organisms appeared to be capable of producing mull through a single ingestion. Rather, large animals appeared to feed on fecal pellets of smaller animals which in turn, ingested fecal material of the larger animals. At each stage the fecal material served as substrate for the growth of microorganisms that were being harvested. Repeated turnover of humus and mineral matrix material by the faunal community appeared to enhance the rate of stable mull formation. Thus the synecology within the various soil systems may be more important than individual species numbers in determining the degree of and rate of mull formation.

It was difficult to assign humus types to the majority of the observed soils since various humus forms were identified in each of the pedons albeit in different proportions. The observed upper organic-rich layers at all sites have the properties described for moder (Kubiena, 1953) humus form. However, a thin well developed mull humus layer was observed in the Southern Tundra and Forest-Tundra Transition region. The Alpine and Montane Prairie sites had moder humus forms although very weak mull fabric i.e. organo-clay complexing, was evident especially in some of the larger fecal pellets. The lower humus layer of the Parkland-Boreal Forest Transition soil had a humus form made up entirely of coalescing humic fecal pellets ranging in size from 30-200 μm and had a mull-like arrangement i.e. a mull-like moder (Kubiena, 1953) fabric. On the other hand, fecal pellets of variable size and largely comprising mull material were present in association with mineral grains and partly decomposed plant fragments as discrete units in moder-like arrangement in the upper Ah of the Parkland soil. This humus-form has also been referred to as mull-like moder (Barratt, 1964) but may best be regarded as a 'proto' mull formation since the soil materials were not completely homogenized.

The most serious problem we have in describing our soils arises from the need to assign a genetic origin for the various fabric sequences. Observed fabrics for upper mineral layers of Tundra soils strongly suggests that mull fabric arrangement (Kubiena's spongy fabric) can arise from processes other than faunal activity such as freezing and thawing. How significant these contributions are to maintaining the tilth of our soils is largely unknown. A better understanding of synecological and soil microfabric relationships is also required if we are to

take maximum advantage of the natural processes within the soil ecosystem to sustain the productivity of the resource base of our land.

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Table 1. Site Characteristics and Surface Soil Micromorphological Features in some Selected Western and Northern Canadian Soils.

1. Northern Tundra Region

Location:	Truelove Lowlands, Devon Island
Landform:	a) Gravelly beach ridge deposits b) well drained soils on ridge top
Vegetation:	<i>Dryas integrefolia</i> and <i>Saxifrage oppositifolia</i> are dominant with some lichens on top of hummocks.
Soil Structure:	Surface layer is an Ahk horizon 10 cm thick with characteristics of a moder humus form. The layer is black (10YR2/1, m) in color and loamy sand in texture. The soil lacks structure and is very friable. Very fine and fine roots are plentiful. The soil material is base saturated with pH 7.2. Organic matter content is 9 percent. The surface layer is underlain by a Bkj and Ck horizon. (For full description see Pawluk and Brewer, 1975a).
Classification:	Orthic Static Brunisol.
Microstructure of Surface Layer:	The moder Ahk horizon has dominantly an ortho-humi-phytogrammic fabric near the surface that grades to an ortho-humigranic fabric with depth (Fig. 1a). Humigranic units range from 20-80 μm in size and are irregular in shape (Fig. 1b). Some loosely bound units of 200 μm size that comprise fine humigranic, orthogrammic and phytogrammic units are also evident (Fig. 1c). Some spores and limestone nodules are present. Matrix is low in clay size mineral components most of which is calcitic in nature.

2. Southern Tundra Region

Location:	Tuktoyaktuk, N.W.T.
Landform:	a) Hummocks of slumped till developed on thermokarst knoll. b) Well drained soil in midslope position.
Vegetation:	<i>Betula glandulosa</i> and <i>Salix arctica</i> with a dominance of feather-mosses and lichens as ground cover.
Soil Structure:	The soil has a 2 cm thick root mat of raw humus with nonvascular plants overlying a 7 cm thick humus layer. The upper moder humus form is somewhat fibrous and matted comprising both semi-decomposed and decomposed plant material. The underlying 3 cm layer has a mull-like moder humus form. The underlying 10 cm thick A(B) horizon is dark brown (10YR3/2, m) clay loam, with friable moderate to strong granular structure. Very fine, fine and medium roots are abundant. The soil is slightly acidic (pH 5) and has 7 percent organic matter in the mineral layer. The A(B) has characteristics of weak mull. (For full description see Brewer and Pawluk, 1975; Pawluk and Brewer, 1975b).
Classification:	Brunisolic Turbic Cryosol.

Microstructure of Surface Layer: The upper moder humus form has an ortho-phyto-humigranic fabric (Fig. 2a). The humigranic units range from 30 to 200 μm in size with a strong distribution around 50 μm . Occasional humigranic units of 350 to 600 μm size are randomly distributed. The lower moder layer has a thick band of mullgranic units 350-400 μm size (Fig. 2b) as well as larger humigranic units up to 900 μm size. The underlying mull-like moder has a phyto-mull-humigranoidic fabric type (Fig. 2c) with a dominance of units of 90-100 μm size some of which are well rounded although larger units (200 μm size) are still present. The A(B) horizon has an upper zone of mullgranic and mullgranoidic fabric with mull units showing strong bimodal size distribution in the 40-120 μm and 400-600 μm (Fig. 2d) size ranges. Smaller units frequently occur within the larger units (Fig. 2e). The lower zone of the horizon has a moderately accommodated mull-matrigranic fabric with well rounded units of 1-2 mm size (Fig. 2f). Accommodation and coalescence increase with depth.

3. Forest-Tundra Transition Region

Location: Inuvik, N.W.T.

Landform: a) Glacial till flutings
b) well drained site.

Vegetation: An open canopy of *Picea mariana*, *P. glauca*, *Betula papyrifera* above an understory of *Rosa sp.*, *Salix sp.*, and *Ledum decumbens*. The groundcover is dominantly *Vaccinium vitis-idaea*, *v. uliginosum*, with various mosses and lichens.

Soil Structure: The soil has an undecomposed leaf mat (LF) 8 cm thick overlying a 3 cm thick largely decomposed moder H layer. Very fine, fine and medium roots are abundant. The organic layer is underlain by a weak mull or mull-like moder Ah horizon 3 cm thick, dark brown (7.5YR3/2, m) in color, silty clay loam in texture and with friable fine to medium granular structure. A 12 cm thick Bm horizon lies below. The soil is moderately acidic (pH 4.5 - 5.2) with 12.2 percent organic matter in the Ah. (For a complete description see Brewer and Pawluk, 1975).

Classification: Brunisolic Turbic Cryosol.

Microstructure of Surface Layer: The lower leaf mat is primarily humi-phytogramic grading to ortho-phyto-humigranic in the H layer (Fig. 3a). Humigranic units are variable in shape and 50-200 μm in size. Fungal hyphae are abundant. Some large (850 μm) humigranic units are also present (Fig. 3b). The Ah horizon largely comprises a mullgranic fabric that grades to a matrigranoidic fabric with depth (Fig. 3c). Minor amounts of humigranic and phytogramic units and zones of mullgranic fabric are also evident. Basic fabric units are 50-90 μm in size although some units of 180-240 μm size are also present (Fig. 3d). Many aggotubules comprising units of the same size and composition are present (Fig. 3e).

4. Boreal Forest Region

Location: Breton, Alberta

Landform: a) Undulating ground moraine.
b) Well drained soil adjacent to stream channel.

Vegetation: Canopy of *Populus tremuloides* and *Picea glauca* with groundcover comprising a mixture of various mosses, lichens and grasses.

Soil Structure: The surface organic layer comprises an undecomposed leaf litter (L) 1 cm thick underlain by a loose to matted semi-decomposed (F) layer 4 cm thick and a well decomposed matted humus (H) layer 1.5 cm thick. Acidity ranges from pH 5 to 6. Very fine and fine roots are plentiful and fungal hyphae are abundant. An Aeh forms the transition to a platy grayish brown (10YR5/2, m) eluviated Ae horizon. (For a complete description see Howitt and Pawluk, 1984).

Classification: Orthic Gray Luvisol.

Microstructure of Surface Layer: The F layer is dominantly phyto-humigranic fabric with partially decomposed plant fragments and humigranic units of variable size (Fig. 4a). Orthogramic f-members are rare to few. The H layer has a few mullgranic units and orthogramic units are more prominent as well. Phytogramic units diminish in importance. Fungal hyphae dominate throughout (Fig. 4b). Fabric units are of variable size (35 μm –1.2 mm) but show strong bimodal size distribution with dominance in the 90-125 μm size range and much fewer in the 600-750 μm size range (Figs. 4c and 4d). All units are largely of the humigranic type but develop a weak mull character near the lower boundary. There is a sharp separation to the underlying Aeh horizon which has a weakly banded mull-matrigranoidic vughy porphyric fabric type. Fine humigranic units occur only in the aggotubules. Small humigranic units are also frequently observed in decomposing plant tissue (Fig. 4e) within all layers.

5. Transition Aspen

Parkland Boreal Forest Region

Location:	Ellerslie, Alberta.
Landform:	a) Glacial Lake Edmonton Plain. b) Imperfectly drained site.
Vegetation:	Open stand of <i>Populus balsamifera</i> and <i>P. tremuloides</i> with a well developed shrub layer of <i>Cornus stolonifera</i> , <i>Rosa sp.</i> , <i>Symphoricarpos albus</i> and minor admixtures of other shrubs. The herb layer comprises <i>Rubus pubescens</i> , <i>Mitella nuda</i> , <i>Mertensia paniculata</i> , <i>Cornus canadensis</i> along with a wide variety of other plants.
Soil Structure:	The surface layer comprises organic horizons 18 cm thick that are characteristic of the moder humus type. The upper partially decomposed litter (LF) is made up largely of aspen leaves. This layer grades into a dark red brown (5YR2/2, m) well decomposed loose, fluffy humus, below. The leaf litter has a near neutral pH and abundant roots of varying size. The organic layer is underlain by a mull-like Ah approximately 35 cm thick. The Ah is black (10YR2/1, m) silty clay in texture, and strong granular in structure. The soil is quite firm and also contains an abundance of roots. Weak mottling is evident in the underlying B horizon. (For a complete description see Sanborn and Pawluk, 1983).
Classification:	Gleyed Black Chernozemic.
Microstructure of Surface Layer:	The F layer has mull-humiphytgranic fabric comprising comminuted plant fragments and an abundance of humigranic units ranging in size from 35 μm to 950 μm . Units of 45 μm size dominate but units of 250-950 μm size (Fig. 5a) are also common. Large (400-600 μm) mullgranitic units are concentrated in horizontal zones that resemble mull-like moder (Fig. 5b). The transition to the H layer shows a decrease in phytgranitic units and stronger coalescence of units of 45 μm size to form a humigranoidic component. The H layer is characterized by humigranoidic fabric of coalesced units dominantly 25-40 μm and commonly 120-180 μm in size (Figs. 5c and 5d). Phytgranitic and orthogranitic components are relatively few. The fabric grades into a humi-mullgranoidic weakly banded fabric in the upper Ah comprising moderately well accommodated, partially fused granitic units of variable size (Fig. 5e). Mullgranitic fabric is better developed at a depth of 3 cm but gives way to mullgranoidic porphyritic fabric with depth. Dominance of larger mullgranitic units generally increases with depth but size of units remains quite variable.

6. Parkland Region

Location:	Hay Lakes, Alberta
Landform:	a) Undulating ground moraine. b) Well drained soil on upper knoll.
Vegetation:	Open stand of <i>Populus tremuloides</i> with a dense ground cover of grasses <i>Festuca stipa</i> , <i>Koeleria</i> and <i>Poa</i> . A wide variety of shrubs and forbes with <i>Rosa</i> dominating are also evident.
Soil Structure:	The near neutral (pH 6.9) surface layer is a well developed black (10YR2/1, m) mull Ah horizon approximately 75 cm thick. The soil is loamy texture (22 percent clay), friable and strong granular. Organic matter content is 9.2 percent. The underlying Bm horizon contains numerous krotovinas and earthworm channels. (For more detailed description see Dudas and Pawluk, 1969).
Classification:	Orthic Black Chernozem.
Microstructure of Surface Layer:	Fabric of the Ah horizon is dominantly humi-mullgranic (Fig. 6a) with phytogranic units more prominent near the surface and with some orthogranic units throughout. Humigranic units are small in size (30-60 μm) while mullgranic units vary from 250 μm to 2 mm in size (Fig. 6b and 6c). There are occasional larger matrigranic units as well.

7. Alpine Region

Location:	Sunshine Basin, Banff National Park, Alberta
Landform:	a) Saddle adjacent to ridge, comprising colluvium/sandstone b) Moderately well drained site on rise of land.
Vegetation:	<i>Phyllodece glanderliflora</i> and <i>Antennaria lanata</i> plant communities comprising a variety of alpine grasses and forbes.
Soil Structure:	The upper layer is a very dark brown (10YR3/2, m) moder grading to mull-like moder Ah horizon 11 cm thick, with silt loam texture and very friable weak fine granular to amorphous structure. Very fine and fine roots are abundant. The soil is moderately acidic (pH 4.8) with approximately 18.9 percent organic matter content. The horizon is underlain by a transition to the Bm. (For full description see Pawluk and Brewer, 1975c).
Classification:	Orthic Sombric Brunisol.
Microstructure of Surface Layer:	The moder humus layer has a humi-phytogranic fabric that grades to phyto-humigranic fabric below. Humigranic units have a size mode ranging from 20-180 μm (Fig. 7a). A few units of 550 μm size are also evident (Fig. 7b). The humus layer is underlain by an organic-rich Ah horizon that has humi-phyto-ortho-mullgranic fabric. The mullgranic units range in size from 20-400 μm (Fig. 7c) and show only weak organo clay complexing. There is a dominance of mullgranic units in the size range of 90-250 μm (Fig. 7d) in the upper zone but becomes better graded with depth. Glass shards, phytoliths and diatoms are common.

8. Intermontane Prairie Region

Location:	Lac du Bois (above Kamloops) British Columbia.
Landform:	a) Morainal drumlin. b) Well drained.
Vegetation:	Middle grassland comprising <i>Agropyron spicatum</i> , <i>Koeleria macranthe</i> , <i>Astragalus miser</i> along with other grassland species.
Soil Structure:	The surface is a very dark gray to black (10YR3/1[d]-2/1[m]) mull-like moder loam with weak fine granular to amorphous structure and very friable consistence (a turf-like feel). This layer is underlain by a Bm horizon. (For a complete description of site see McLean, A. 1982).
Classification:	Orthic Dark Brown Chernozem.
Microstructure of Surface Layer:	The fabric of the Ah is dominantly ortho-humigranic and granoidic with a minor chlamydic component (Fig. 8a). Humigranic units have a strong modal size in the 25 μm range (Fig. 8b) but few larger units 90-200 μm size and very few units of 450-600 μm size are also present (Fig. 8c). Very few phytogranic units are also found. Mullgranic units are notably absent although under high magnification humigranic units appear to have a weak mull-like character.

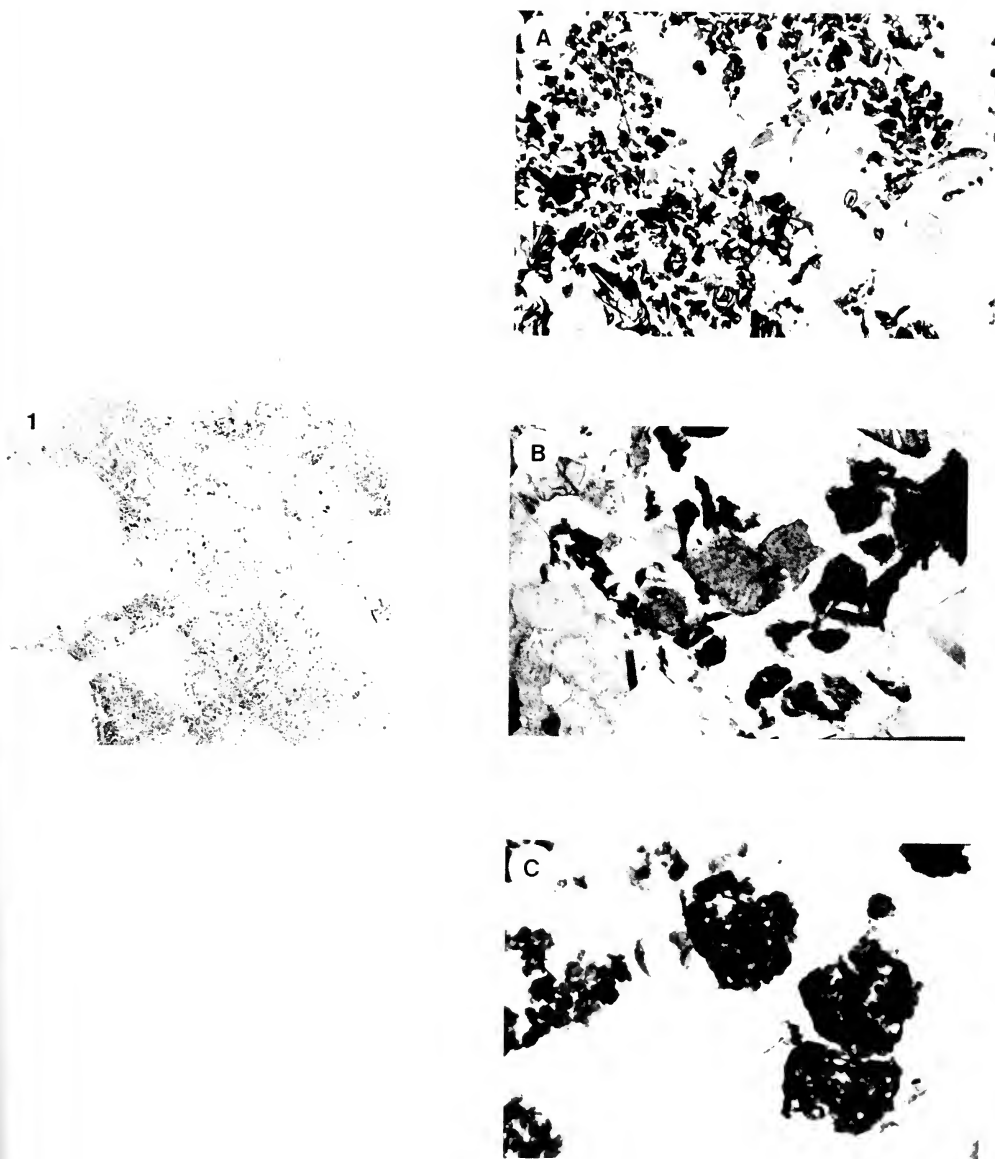


Fig. 1. Fabrics of moder humus from an Orthic Static Brunisol, Devon Island, Northwest Territories, Canada.- (a). Ortho-humigranic fabric (x30m); largely fecal pellets of microarthropods. (b). Humigranic units comprising fecal pellets 20-80 μm size (x150m) likely from collembolans and/or enchytraeids. (c). Loosely bound humigranic units 200 μm in size; probably enchytraeid cast (150xm).

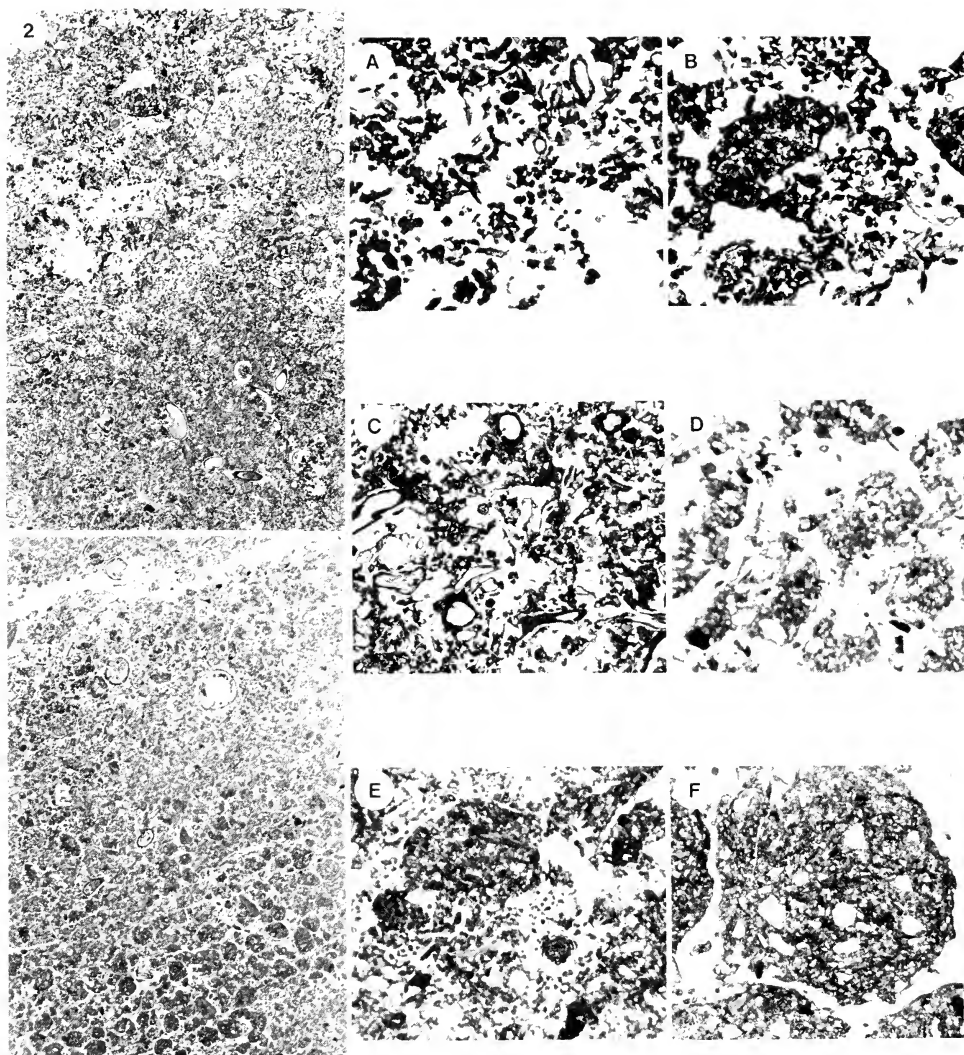


Fig. 2. Fabrics from the humus-rich layer of Brunisolic Turbic Cryosol, Tuktoyaktuk, Northwest Territories, Canada.—(a). Ortho-phyto-humigranic fabric (x30m); humigranic units show strong modal distribution of $50\ \mu\text{m}$ and appear to be largely droppings of collembolans and enchytraeids. (b). Large fecal pellets ($400\text{--}600\ \mu\text{m}$) (x30m) of dipterous larvae and/or diplopods. (c). Phyto-mull-humigranoidic fabric (x30m); dominance of fecal material $90\text{--}100\ \mu\text{m}$ in size comprising humus and mineral constituents, believed to be droppings of collembolans. (d). Larger mullgranic units ($400\text{--}600\ \mu\text{m}$) in the A(B) horizon (x30m). (e). Smaller mullgranic units ($40\text{--}120\ \mu\text{m}$) associated with larger units in the A(B) horizon (x30m), probably fecal pellets of collembolans and/or enchytraeids. (f). Large mull-matrigranic units ($1\text{--}2\ \text{mm}$) (x30m); possibly fecal pellets but more likely formed through frost processes.

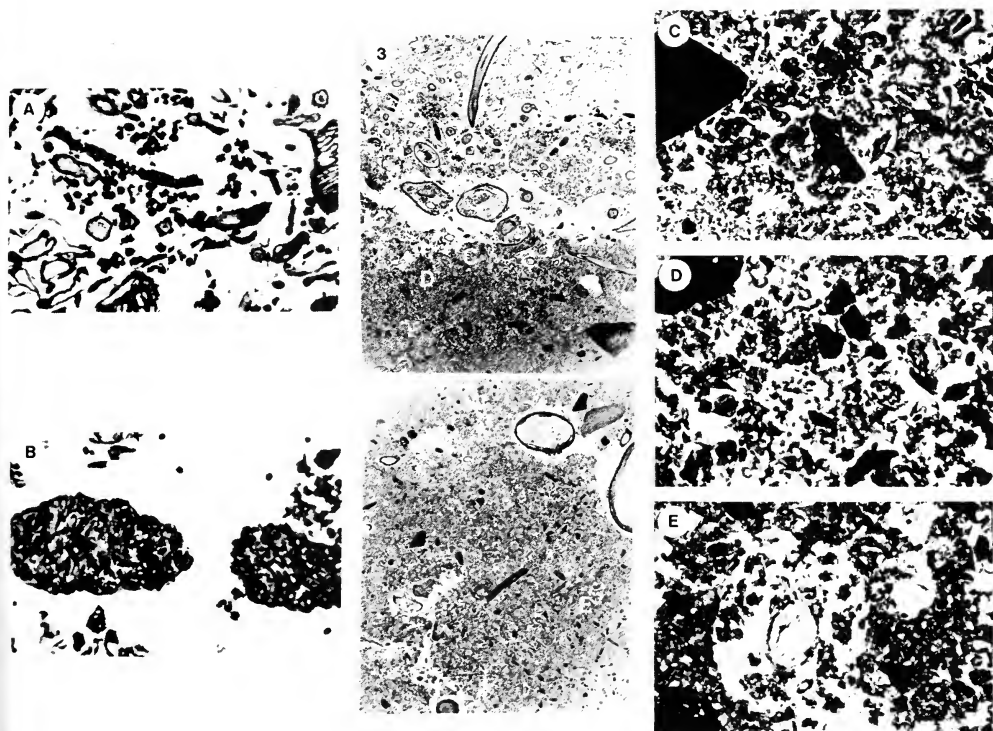


Fig. 3. Fabrics from the humus-rich layer of Brunisolic Turbic Cryosol, Inuvik, Northwest Territories, Canada.— (a). Ortho-phyto-humigranic fabric of the H layer (x30m). Majority of humigranic units are 50 μm in size and are likely fecal pellets of collembolans; larger casts of 90-120 μm size are likely those of enchytraeids. (b). Large fecal pellets (850 μm) of humic material (x30m) likely droppings of dipterous larvae. (c). Mullgranoidic fabric of the Ah horizon (x30m). Basic units are 50-90 μm size with some units 180-240 μm size also evident. The smaller units are likely fecal pellets of enchytraeids and/or collembolans. (d). Same as (c) (x50m). (e). Aggrotubule with fecal pellets (x50m).

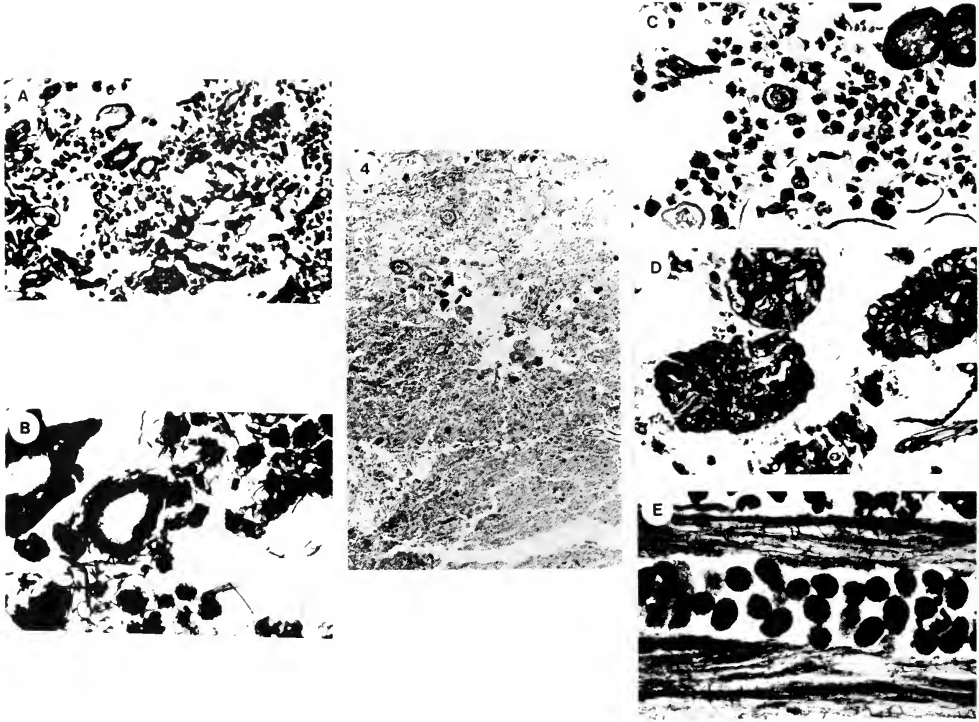


Fig. 4. Fabrics from the organic layer of an Orthic Gray Luvisol, Breton, Alberta, Canada.— (a). Phyto-humigranic fabric of the F layer (x30m). Fecal pellets are dominantly 50 μ m size possibly from collembolans. (b). Abundant fungal hyphae intimately associated with fecal pellets (50-60 μ m) and plant fragments (x150m). (c). Zone of humic fabric with a dominance of fecal pellets 90-125 μ m size (x30m). Regularity in the shape of the units suggests casts of collembolans although other animals cannot be discounted. (d). Zone of humic fabric with a dominance of fecal pellets 600-750 μ m size (x30m). Their presence likely reflects the activity of dipterous larvae and/or small earthworms. (e). Fecal pellets (25 μ m) of acarines in decomposing plant tissue (x150m).

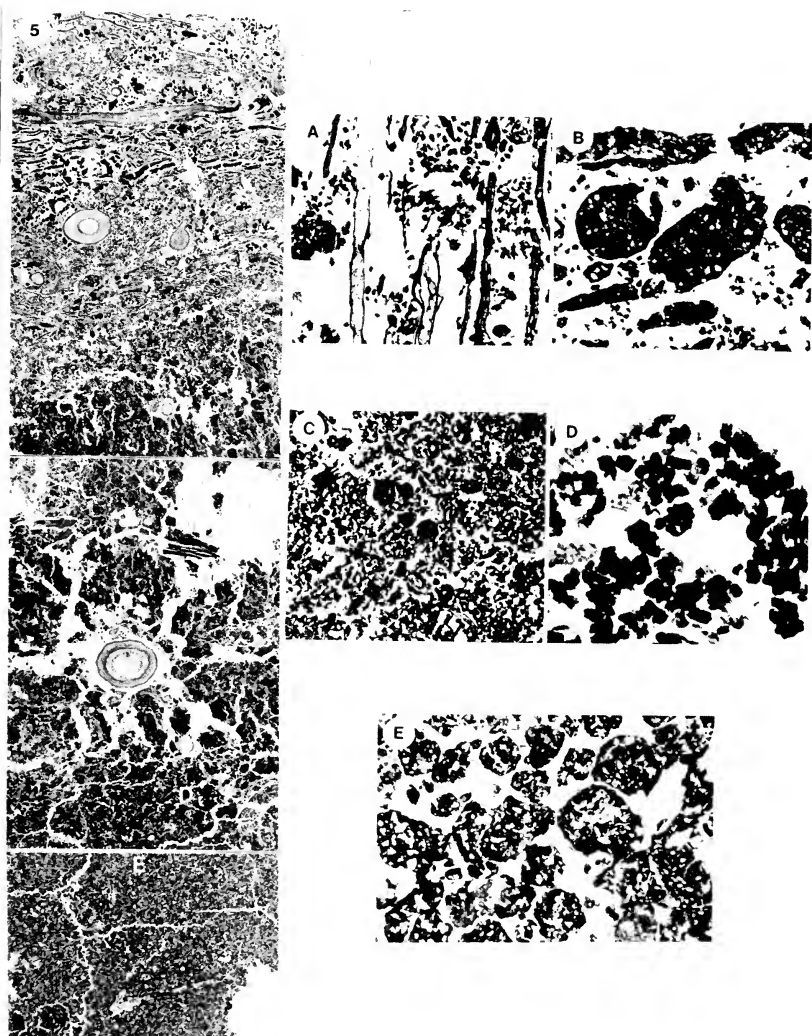


Fig. 5. Fabrics from humus-rich layers of Gleyed Black Chernozem, Ellerslie, Alberta, Canada.— (a). Mull-humi-phytgranitic fabric of the F layer (x30m). Small humigranitic units (35 μm) are fecal pellets of microarthropods, the larger units (350-400 μm) are likely fecal pellets of diplopods. (b). Mullgranitic units (400-600 μm) in the upper H layer are likely diploid casts (x30m). (c). Humigranoidic fabric of the lower H layer (x30m). Units of fabric comprise entire and decomposing small fecal pellets (25-40 μm) of small arthropods and larger fecal pellets (120-180 μm) possibly of isopods and/or enchytraeids. (d). Discrete and decomposing fecal pellets of collembolans and/or enchytraeids in c) under high magnification (units 25-40 μm size). (x150m). (e). Humi-mullgranoidic fabric of the Ah with units dominantly 450-500 μm size (x30m). Units are porous and appear to comprise smaller fecal pellets reorganized through frost processes.

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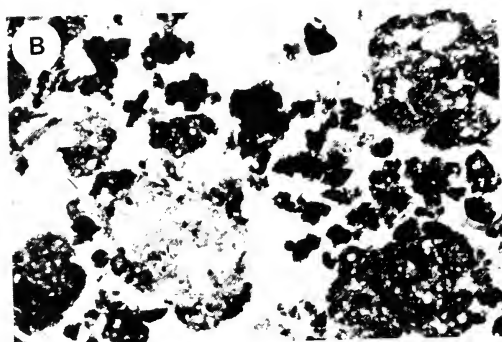
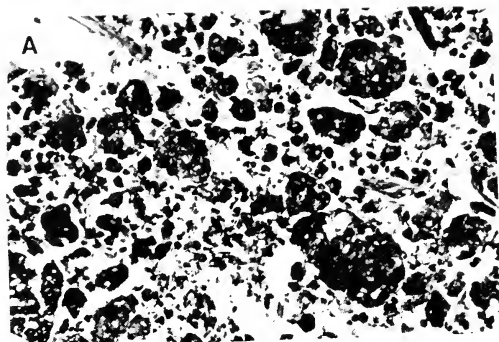
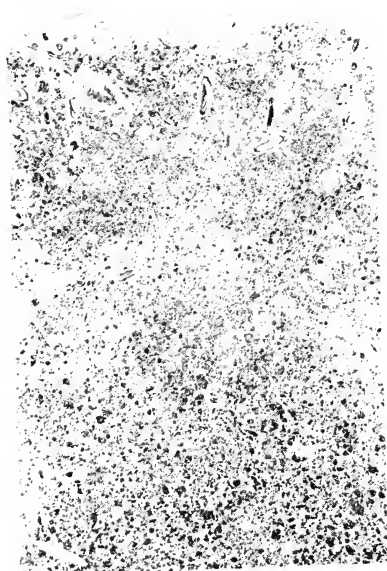


Fig. 6. Fabrics of Ah horizon from an Orthic Black Chernozem, Hay Lakes, Alberta, Canada.— (a). Humi-mullgranic fabric from the Ah (x30m). Fecal pellets vary in size from 30 μm to 400 μm . Smaller units are humigranic. (b) Small humigranic and larger mullgranic units of fabric from the Ah (x50m) ppl. Note uneven distribution of clay and humus in plasma. (c) Same as (b) in plain light.

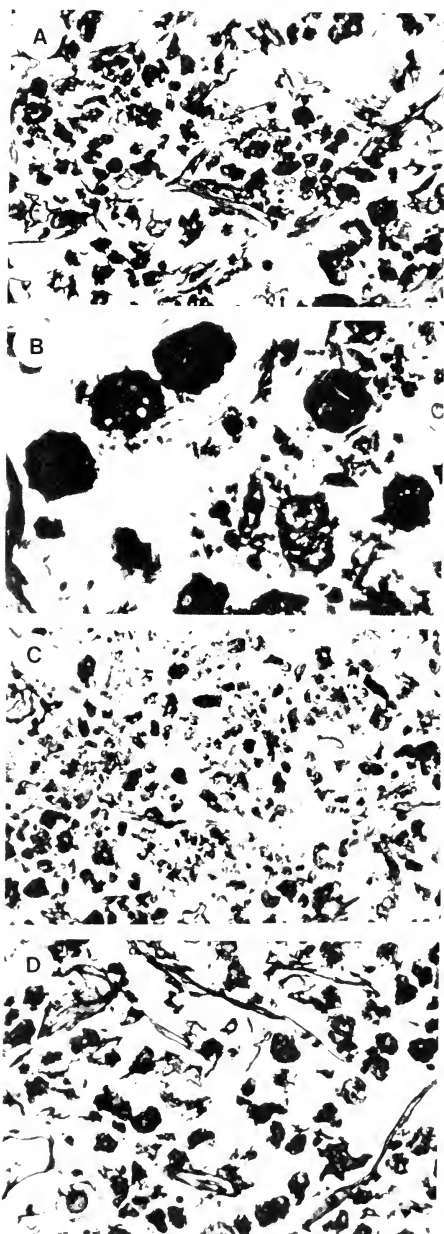


Fig. 7. Fabrics of humus-rich layers of Orthic Sombric Brunisol, Sunshine Basin, Alberta, Canada.— (a). Phyto-humigranic fabric in moder humus layer (x30m). Humus fecal pellets range in size from 20-180 μm and probably reflect activity of collembolans and enchytraeids. (b). Fecal pellets comprising humic material and silt grains in same layer as a). Large units (450-550 μm) are probably casts of Diplopoda (x30m). (c). Humi-ortho-mullgranic fabric in Ah. Mullgranic units range from 20-250 μm (x30m). (d). Mullgranic units in Ah 90-250 μm in size (x30m) possibly collembolans and/or enchytraeid fecal pellets.

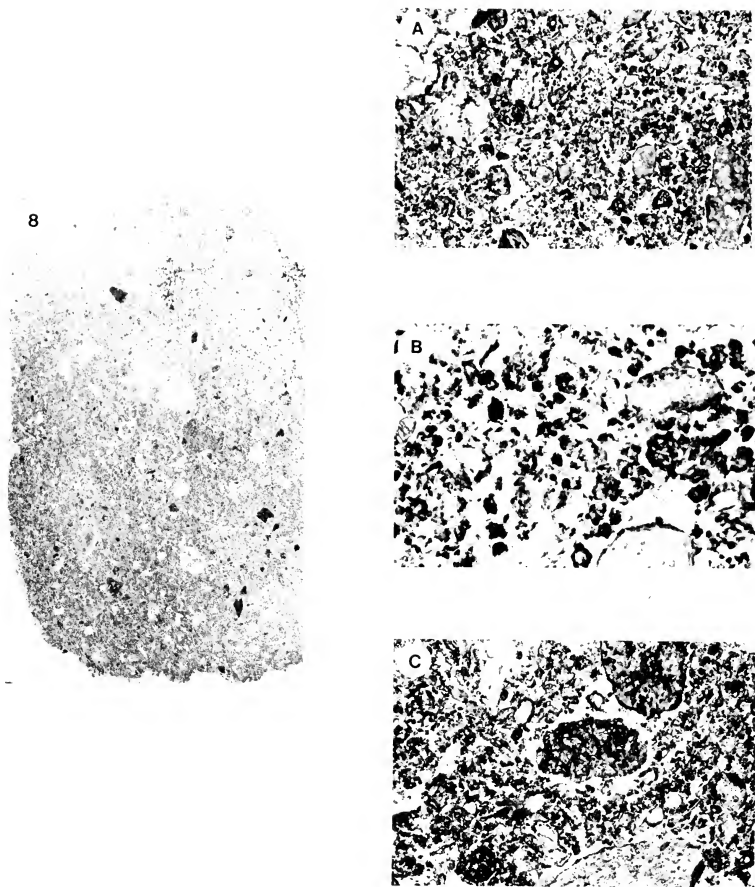


Fig. 8. Fabrics of Ah horizons of Orthic Dark Brown Chernozem, Lac du Bois, British Columbia, Canada.— (a). Ortho-humigranic fabric with Chlamydic component in Ah (x30m). (b). Humigranic units dominantly 25 μm size (x150m) probably fecal pellets of microarthropods. (c). Fecal pellets 450-600 μm size probably of diplopods (x30m).

SOIL MICROSTRUCTURES - CONTRIBUTIONS ON SPECIFIC SOIL ORGANISMS

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ABSTRACT

The soil zoological approach to the soil micromorphological studies is described. The ecological methods, e.g., synecological analysis of soil animal communities, succession of soil animals, autecology, etc. are determined as basic methods for evaluating soil thin sections from soil-zoological point of view. The role of soil animals in formation of soil microstructure is divided into three basic categories: A) disintegration of dead organic matter, B) formation of zoogenic microstructural soil matrix, and C) tunnelling and burrowing activities of soil animals. The role of different groups of soil animals in disintegration of dead organic matter is described and the characteristic features are documented on soil thin section figures. The characteristic microstructural features of humus development during the succession are described. The short term processes of decomposition (disintegration) in humus profile relate to the long term development of humus form during the succession as does ontogeny to phylogeny in the animal kingdom in Heckel's biogenetical law. The droppings of different groups of soil animals are described from the morphological point of view and their location in the soil profile is given.

RÉSUMÉ

L'auteur décrit la méthode pédo-zoologique d'étude de la micromorphologie des sols. Les méthodes écologiques, telles que l'analyse synécologique des communautés animales des sols, la succession des animaux des sols, l'autécologie, etc., sont considérées comme des méthodes de base pour l'évaluation des coupes minces de sol d'un point de vue pédo-zoologique. Le rôle des animaux des sols dans les processus de formation de la microstructure des sols se divise en trois catégories fondamentales: A) désintégration de la matière organique morte, B) formation de la matrice microstructurale zoogénique, et C) percement de tunnels et fouissage par les animaux endogés. L'auteur décrit le rôle de différents groupes d'animaux des sols dans la désintégration de la matière organique morte et en présente les traits caractéristiques sur des figures de coupes minces de sols. Il décrit aussi les traits microstructuraux caractéristiques du développement de l'humus durant la succession. Les processus de décomposition (désintégration) à court terme ayant lieu dans la couche d'humus sont en rapport avec le développement à long terme du type d'humus au cours de la succession de la même façon que l'ontogénie l'est à la phylogénie chez les animaux, tel que le rapporte la loi biogénétique d'Heckel. Finalement, l'auteur décrit les excréments de différents groupes d'animaux des sols d'un point de vue morphologique et indique leur emplacement dans le profil du sol.

INTRODUCTION

Micromorphological methods of soil investigation were originated and developed by Kubiena as a soil biological approach to pedological problems. They were used in soil biology in the 40's and 50's by Kubiena (1943, 1948, 1955) and his collaborator Kühnelt. Primarily

through the contributions of pedologists, geologists, and to a lesser extent by the soil biologists, method, theory and nomenclature of soil micromorphology were further developed in the 60's and 70's, when soil micromorphology became an independent branch of pedology. In spite of important publications using soil micromorphological methods, the number of soil biologists using these methods has been and is still very low and does not reflect their present and future importance. This international meeting of soil zoologists, soil micromorphologists and pedologists is an important step in collaboration among specialists of these ecological branches. Only by such an interdisciplinary collaboration is it possible to obtain new and untraditional views on soil and on complicated, dynamic soil processes.

Soil micromorphology has already helped to solve some practical problems in soil biology. It is possible to use it for monitoring man's impact on the environment, for solving practical questions connected with soil fertility and recultivation, for solving theoretical problems of soil development, *et cetera*.

The literature about soil micromorphology contains some contradictory results. My contribution summarises and discusses both my own and published results dealing with the role of soil animal groups in forming soil microstructures. A wider examination of these problems enables better understanding of ecological patterns in formation of microstructure and in soil development generally. For this reason my contribution also includes soil micromorphological methods from a soil zoological viewpoint. One part is devoted to the diagnosis of the tracks of soil animal activities in the soil. Some unsolved or controversial questions will also be pointed out, to stimulate work in some new directions.

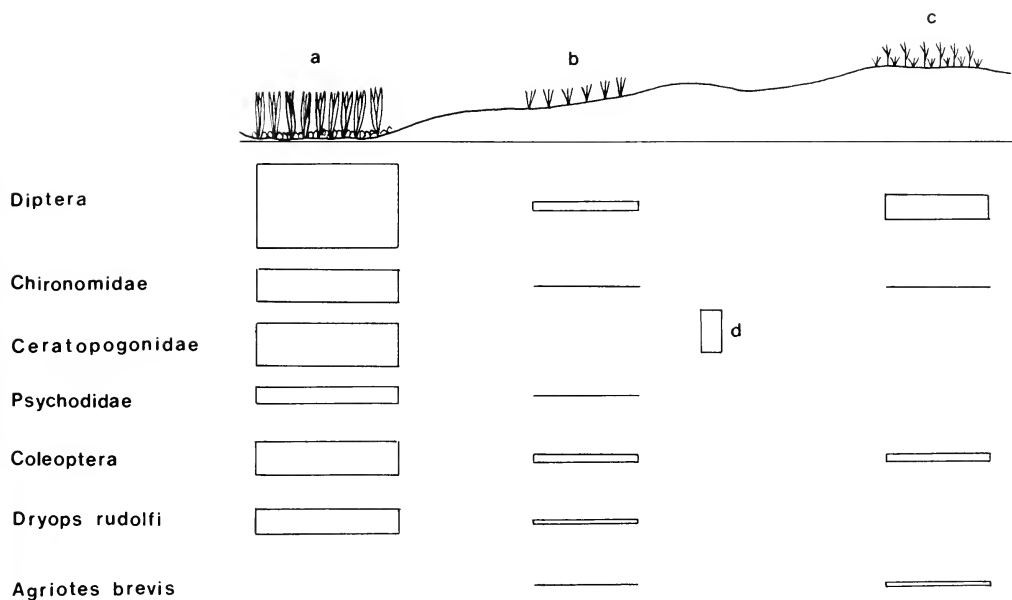
My own results are from soils in the temperate, subpolar, alpine and mediterranean zones and from some subtropical and tropical soils in Cuba.

METHODS

Methods of preparing thin sections of soil and their morphometric evaluation are well described in the book edited by Jongerius (1964). Methods for evaluation of soil thin sections from the soil zoological point of view are more complicated due to the difficulty of determining the origin of the zoogenous microstructures.

To determine the zoogenous microstructural components of the soil we must start from the coenological analysis of the zoedaphon in the soil under study, from the food requirements of the dominant species of the soil meso-, macro- and megafauna, from the shape and size of faecal pellets obtained in the laboratory, from newly captured animals, and from direct observation of some dominant species in the field.

The coenological analysis of soil animal communities enable determination of the dominant species in the soil under study. In the second step we identify the predators, phytophagous and microphagous species which do not play a direct role in processes of soil microstructure formation. For questionable taxa, it is necessary to analyse the gut content to establish the roles of such species in forming the soil microstructure. It is important to point out that populations of some soil animals have synchronised food consumption and that such animals (*e.g.*, Collembola) do not feed during certain life periods (ecdysis). For such animals, it is necessary to analyse the gut content repeatedly. Some soil animals appear in high numbers only in some parts of the year (*cf.* Rusek, 1984), also important to remember in evaluating the role of such animals in the soil forming processes.



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Fig. 1. Distribution of different groups of soil insects in a swampy meadow (a), wet meadow (b) and dry meadow (c) in a periodically inundated area in South Moravia. Height of d - 1000 specimens. m^{-2} . Larvae of some groups of Diptera and *Dryops rudolphi* play an important role in processes that form soil microstructure in the swampy meadow.

To obtain droppings of soil animals known to affect processes of soil formation (gut filled with brown or black particles of dead organic matter in different stages of disintegration and mostly mixed up with mineral particles), immediately after extraction in the Tullgren apparatus the animals are placed into glass jars with wet filter paper on the bottom. It enables us to identify the zoogenous microstructures in soil thin sections with particular species of soil animals. In a further phase, laboratory rearings of the species forming the soil microstructure are carried out to prove their food requirements. In the future we will have enough experience to limit this long procedure to the coenological analysis of particular groups of soil fauna and of other dominant decomposers for which a role in the processes of formation of microstructure are still not established. We may also obtain valuable results by direct observation of soil animals in the field, as is pointed out by Kubiena (1964), Zacharie (1965), Bal (1970) and others. But the importance of many of the soil animals cannot be established by field observation.

SUCCESSION OF SOIL TYPES DURING SUCCESSION OF WHOLE ECOSYSTEMS

The coenological composition of soil fauna and the presence of different groups and species of decomposers in the soil has a crucial effect on the rate and forms of disintegration of dead organic matter. The composition of soil fauna coenoses, together with some other factors, determines what humus form, soil microstructure and soil type will develop in the ecosystem. In

my contribution (Rusek, 1978) the connections between successional development of plant communities, soil animal communities and soil types were shown. Soil animals play an active part in the development of soil and whole ecosystems. Soil animal communities are developing and changing during succession, and in association with them the succession of humus forms proceeds as well (Rusek, 1978).

Each soil type has its own, characteristic soil fauna (Fig. 1) a fact which enables us to use soil animals for soil diagnostic purposes (Ghilarov, 1965). It is known that the most developed humus form, the mull, is formed by earthworms. But only some ecological types of earthworms, the endogeic and the anecic ones, form the mull. The epigeic type of earthworms form typical moder. The zoogeographical distribution of earthworms plays an important role in mull distribution. Mull cannot be formed in areas where the aceic and endogeic earthworms are missing; such areas include the Arctic and parts of the boreal zones, as well as initial and little developed soils. In these areas or soil types, only less developed forms of humus (e.g., raw humus, microarthropod moder, arthropod moder, etc.) occur. These ecological and zoogeographical rules and dependences in soil and humus development must be kept in mind in evaluating thin sections of soil.

During soil succession many important changes in composition of species and of ecological groups of soil fauna occur. In the first developmental stages usually only microarthropods (Collembola, Acarina) play an important role in processes of formation of soil microstructure, and the microarthropod moder is formed by them. Some soils reach only this developmental stage as a climax. These soils occur most commonly in the Arctic and in the alpine zones. In temperate, subtropic and tropic zones the humus develops to more complex forms, and determination of its micromorphological components is more difficult because of the great diversity of soil animals taking part in its development.

ROLE OF SOIL ANIMALS IN PROCESSES OF FORMATION OF SOIL MICROSTRUCTURE

We may divide processes of soil microstructure formation into three basic categories from the soil zoological point of view:

- (a) disintegration of dead organic matter
- (b) formation of zoogenic microstructural soil matrix, and
- (c) tunnelling and burrowing activities of soil animals.

Disintegration of dead organic matter

The main source of dead organic matter used in processes of formation of the zoogenous soil microstructure is the plant litter. Before disintegration, the litter is intensively invaded by soil microflora and soil microfauna, and only after a certain period is it attacked by larger soil animals and disintegrated step by step. Some species of microarthropods (Collembola, Oribatei) and enchytraeids skeletonize the leaves between the veins only, causing Fensterfrass, whereas larvae of some Mycetophilidae, Lycoridae and other Nematocera also eat the thinner ribs, causing Lochfrass (Figs. 2, 3). Diplopods (*Glomeris* spp., *Julus* spp., etc., Marcyzzi, 1970), isopods and some earthworms bite off larger pieces of leaf tissue together with the thinner ribs. The large midrib of oak leaves is mined by *Rhisotritia minima* (Berlese Oribatei) [after Bal, (1968, in Harding and Stuttard, 1974 and Bal, 1970)].

The litter of conifers is disintegrated more slowly and with more difficulty. Parenchymatic tissues are eaten by phthiracarid mites (Oribatei) which leave typical droppings in the bitten

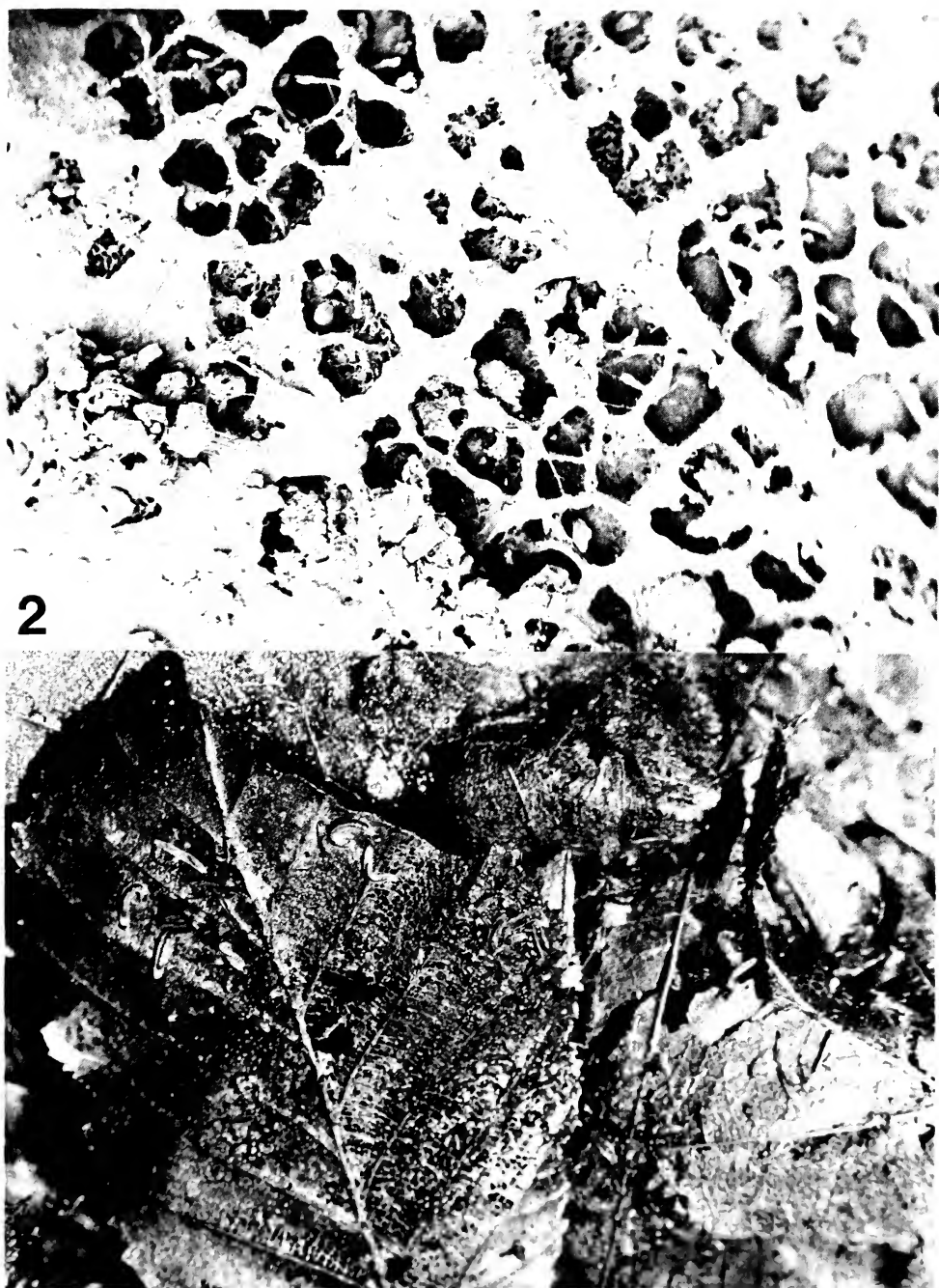


Fig. 2. Oak leaf partly disintegrated by larvae of Mycetophilidae. Their pellets (on the left side) invaded by nematodes.
Fig. 3. Mycetophilid larvae disintegrating leaf litter.

off hollows inside the needles. The needles in the litter layer are also disintegrated by larvae of Tipulidae and Mycetophilidae, caterpillars of *Adela* spp. (Bal, 1970) and by some earthworms (Zachariae, 1966).

Wood disintegration has been studied by many authors, but we only have little data about the zoogenous micromorphological processes in rotting wood (cf. Babel, 1975). Fallen twigs and dead roots are invaded by phthiracarid mites which feed on the rotten wood. In thin sections of soil, we can see large hollows filled by ovoid droppings of these animals (Fig. 4). Often, the periphery of the hollow near the bark is covered by droppings of bark beetles (Scolytidae) secondarily eaten by phthiracarids (Fig. 5). I have observed a few invasions of Collembola (*Mesaphorura* spp.) in the wide, opened hollow of twigs. In such openings, the phthiracarid pellets are mixed with dark Collembolan droppings containing small mineral particles (Fig. 4).

The wood of the tree stumps and logs is disintegrated first by xylophagous larvae and some adults of beetles such as Scolytidae, Curculionidae, Buprestidae and Cerambycidae. When the rotting processes have been advanced, the wood is attacked by larvae of Nematocera (Tipulidae, Mycetophilidae, Lycoridae, etc.) and some Lucanidae, Cetoniidae and Dynastidae. The tracks and pellets of these animals are of typical shape, composition and size, but the micromorphological diagnostic characters have not yet been described. After some years a typical soil fauna invades the rotten wood. The pellets of the xylophages are then disintegrated and mixed step by step with mineral particles. Microarthropods, enchytraeids, macroarthropods and some earthworms contribute to this process. In subtropical mountain rain forests in Cuba, larvae and adults of *Passalus* sp. (Coleoptera: Passalidae) play an important role in wood disintegration. After passing through the gut the pieces of wood in the excrement are invaded by special microflora and the droppings are then again eaten by larvae of the same species or other xylophagous animals. In the tunnels of these animals it is easy to distinguish light coloured pellets after the first passage through the gut and the brownish or black ones which passed through two or more times. These droppings then become a food source for a diversified community of soil animals of different size.

Zoogenic formation of the soil matrix microstructure

Through the feeding activity of soil animals, the plant litter is disintegrated and converted into new structures which may be stable or which are further converted by aging or feeding activities of other soil animals, into other microstructures characteristic of the soil matrix. Like the successional development of soil types, the development of humus forms also occurs in successive steps. This successive development has its own regularities connected with the ecology of soil animals from the decomposer ecological group. We may follow the progressive development of humus forms during litter disintegration and during incorporation of the new microstructural elements into the soil matrix. These short term decomposition processes in the humus profile relate to the long term humus form development during succession as does ontogeny to phylogeny in the animal kingdom in Haeckel's biogenetical law. Also this short term development of humus forms in the soil profile has its own regularities which may be observed in, for example, forest soils.

The simplest humus form in xeric succession is the microarthropod moder formed by droppings of Collembola, Oribatei and some small nematoceran-larvae (Diptera) (Rusek, 1978). The next developmental step is the arthropod moder formed mainly by the larger animals belonging to the group of macrofauna (Diplopoda, Isopoda, larvae of Diptera and Coleoptera), by the enchytraeids and by the small epigeic forms of earthworms living in the

litter (e.g., *Dendrobaena rubida*, *Eisenia foetida*, etc.). The arthropod moder is microstructurally heterogenous in comparison with the microarthropod moder. The mull-like moder has more complicated structure. The highest form of humus is mull and it develops only when succession reaches a level at which conditions enable high densities of anecic and endogeic earthworms.

Litter disintegration in a forest soil usually starts with the feeding activity of Collembola, Oribatei and small larvae of Diptera. Their pellets belong to the microarthropod moder and they are readily distinguishable in the uppermost litter layer (Fig. 6). "Later" and deeper in the same litter layer are the larger pellets of enchytraeids, diplopods, larger Diptera larvae, etc. belonging to the moder. Microarthropod droppings are also formed in this layer, but they are almost completely consumed by the macroarthropods and incorporated into their faecal pellets. In some larger pellets they are easily visible in soil thin sections (Fig. 8). The macroarthropod droppings can be secondarily disintegrated by aging into the small, original pellets of microarthropods (Fig. 8). When anecic and endogeic earthworms are present in the soil in high densities, the picture of processes of formation of arthropod moder can be completely obscured by the mull production of these lumbricids. The droppings of macro- and microarthropods are then totally disintegrated and mixed with mineral particles in the guts of these animals (Fig. 7).

The nomenclature of humus forms relates to the whole humus profile; the name of the humus form is derived from the prevailing microstructural elements in the profile. It is difficult to decide what humus form occurs in many samples of certain soil profiles. It is proposed here to identify the humus form in each subhorizon of the L- and F- horizons.

Disintegration of larger droppings by the soil mesofauna (enchytraeids, Collembola, etc.) is of great importance in the microstructural forming processes. It is most remarkable in the upper part of the H-horizon, where the large, spongy droppings of earthworms are eaten by enchytraeids and transferred into their small droppings (Zacharie, 1965). The same is true for some Collembola (e.g., *Onychiurus* spp., Tullbergiinae gen. spp.,) (*Folsomia* spp.) (Fig. 8). The macroarthropod droppings in the F-horizon are disintegrated in the same manner as described by Zachariae (1964) for enchytraeids and by Dunger (1983) for Collembola.

Tunnelling and burrowing activities of soil animals

Only soil animals from decomposer ecological groups play a part in the above described disintegration processes. Tunnelling and burrowing are also done by animals from other ecological groups such as herbivores, predators, etc. These have usually well sclerotized bodies, strong mandibulae, head capsules and urgomphi, feet adapted to life in soil, well developed muscles, worm-like shapes, etc. They aerate the soil profile by their tunnelling activities when moving through the soil in search of food, reproductive or hibernation sites, etc. In autumn, the wireworms (Elateridae) injurious to cultivated plants, move 50–60 cm deep to hibernate. They migrate to the soil surface the following spring during which time they make long horizontal channels in the uppermost part of the soil, searching for the roots of the host plants (cf. Rusek, 1972). There is a great diversity of actively tunnelling soil animals within the soil macro- and megafauna, but some species of the soil mesofauna may also make active microtunnels in the soil matrix (e.g., some Collembola from the family Onychiuridae, oribatid mites, enchytraeids). Many of the tunnellers mix the organic matter with mineral particles and translocate the droppings between soil horizons up to the soil surface. During such activities the organic matter may be translocated by earthworms deep into the mineral horizon and the mineral soil components transported to the surface. Soil material is translocated by earthworms, especially



Fig. 4. Soil thin section from a moder rendzina. Pellets of oribatid mites (o) and Collembola (c) inside the small twig, and droppings of enchytraeids (e). Fig. 5. Disintegration of twigs in a moder, by bark beetles and oribatid mites: droppings of these animals are indicated by (s) and (o) respectively.

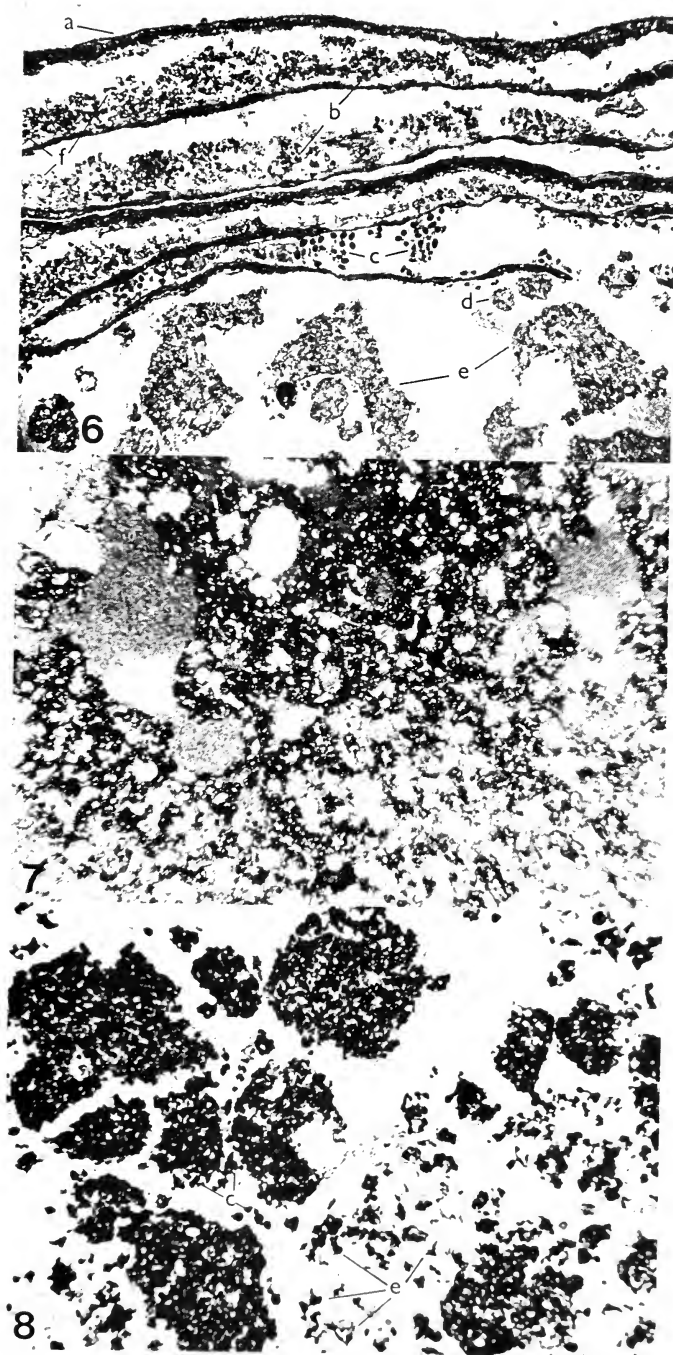


Fig. 6. Oak leaves (a) partly disintegrated by Collembola (f), Enchytraeidae (b), oribatid mites (c). Below the leaves droppings of nematoceran larvae (Diptera) (d) and of the epigeic earthworm *Dendrobaena rubida* (r). Moder rendzina, Bohemian Karst. Fig. 7. Spongy droppings of an endogeic earthworm, mull. Fig. 8. Droppings of epigeic earthworms subsequently disintegrated by enchytraeids (e) and Collembola (c).

the anecic ones, and also by groups such as ants and some other Hymenoptera, termites dung beetles, some crickets and other insects. The cast-forming activity of anecic earthworms, ants and another animals is well known and of great importance in microstructural and soil forming processes. The zoogenous microstructural cavity system has been analysed in soil thin sections only by a few workers (e.g., Babel and LeNgoc, 1977) and deserves more attention in the future. It is easier to analyse these activities using thick soil sections or on ground block sections than using thin sections of soil.

Because of their macromorphological impact, the burrowing and tunnelling activities of vertebrates were not mentioned in connection with soil microstructure processes. The activities of some groups of the invertebrate soil macro- and megafauna also extend to a macromorphological level during soil succession.

STRUCTURE OF ANIMAL DROPPINGS IN THE SOIL MATRIX

The most important contribution of soil animals to formation of the microstructural fabric is their excrement, also called droppings, pellets or faecal pellets. These are the prevailing primary aggregates of many humus horizons. Each group or even species of soil animal produces droppings of characteristic shape, composition, size and colour (cf. Bal, 1973). Location and accumulation within the soil profile are also important features aiding in the determination of the origin of droppings. Some droppings are very stable for a long time, especially in rendzina soils, but usually they change with age or through feeding activities of secondary decomposers. Many taxonomically different groups of soil animals produce similar pellets, which consequently may be misinterpreted in soil thin sections. As was stated in the methodological section, the determination of droppings must start from the coenotical analysis of the soil fauna. The diagnostic features of droppings of the most important soil forming animals groups are described below. The droppings of well known groups as well as groups for which we lack information are described briefly.

Droppings of Oribatei

Pellets of oribatid mites (Oribatei, Acarina) are very distinctive and, in most, are easily recognizable microstructures in the soil matrix. Their characteristics have been described by many authors (e.g., Zachariae, 1965; Bal, 1970; Rusek, 1975): egg-shaped or sphaeric, with smooth surface, very compact and without mineral particles inside, light brown coloured and up to $200 \times 140 \mu\text{m}$ in size, depending on the species and the instar of the mite. Most characteristic are the smooth surface and the missing mineral particles. These two characters are conditioned by the structure of these mites. They have a very narrow pharynx through which mineral particles and larger pieces of food cannot enter the gut (Taraman, 1968). In the ventriculus the ball of food particles is covered by a thick peritrophic membrane (Fig. 9) which also covers the droppings, giving them their smooth surface. Taraman (1968) mentions that the faecal pellets of some oribatid species are grayish or black; their colour may shift from yellow to black during aging, due to the action of microorganisms. The same author notes that pellets of *Steganacarus magnus* fed on wood tissue do not have a smooth surface. These facts may explain why oribatid excrements were not recognized in soil thin sections from places where the macrohumiphagous Oribatei live in high densities.

The oribatid droppings are usually found in groups between the leaves in the L-layer, inside coniferous needles (Fig. 10) or in feeding cavities in rotten wood (Fig. 4). Often groups of

droppings of different size are together in one hollow, indicating the moulting cycle of the feeding animal. Macrohumiphagous species from the oribatid family Phthiracaridae are most important in the processes of formation of soil microstructure, but we may also find species in other families contributing to these processes. Oribatid mites occur in all soil horizons.

Droppings of Collembola

Collembola are one of the most abundant representatives of soil mesofauna. They belong together with Acarina and some smaller groups of Tracheata to the group of microarthropods. Quite contradictory data have been published about the importance of Collembola in processes of formation of soil microstructure. Zachariae (1963) is of the opinion that Collembola do not play an important role in the disintegration of organic matter and in the processes of formation of soil microstructure. But previously Kubiena (e.g., 1955) has pointed out the leading role of Collembola in forming some mountain soils (e.g., pitchmoder rendzina). Also Bal (1970), Dunger (1983) and other authors have shown the importance of Collembola in litter disintegration. Kubíková and Rusek (1976) have established that in a xeric protorendzina profile the droppings of Collembola predominate. Rusek (1975) describes the pellets of Collembola, Oribatei and Enchytraeidae and the differences between them.

The droppings of Collembola are usually compact, 30–90 μm in diameter (over 100 μm in larger species), irregularly round, with rugged, irregular surface, usually containing mineral particles, and usually black. The remains of organic matter inside them do not contain larger parts of plant tissue. They clearly differ from the smooth, egg-shaped and light brown oribatid droppings.

Collembola are one of the most ecologically diversified groups of arthropods and this fact has given rise to a lack of understanding of their function in the soil by some authors.

There are Collembola living atmobiologically on higher plants and some of them are even important pests (Fig. 11) (e.g., *Sminthurus viridis*). The epigeic forms are living on the soil surface and in litter and some species are important litter decomposers (e.g., *Tomocerus* spp. (Fig. 12), *Orchesella* spp. (Fig. 13), *Isotoma* spp., *Hypogastrura* spp.). The hemiedaphic species live in the litter and F-horizon, whereas the euedaphic ones are in the F- and H-horizons. Some of the hemiedaphic as well as euedaphic species contribute to the processes of formation of soil microstructure (e.g., *Folsomia* spp., *Onychiurus* spp., *Mesaphorura* spp., *Megalothorax minimus*, etc.).

In the Collembola strongly developed feeding specialization exists. We recognize Collembola with sucking mouth parts (*Neanura* spp., *Micranurida* spp., etc.), predators (*Friesea* spp., *Cephalotoma grandiceps*), fungivores (*Pseudosinella* spp., *Paratullbergia callipygos*, etc.), macrophytophages (*Sminthurus* spp., *Bourletiella* spp. (Fig. 11), etc.), detritivores and other specialists. It is no wonder that any one who observed a phytophagous or microhumiphagous species arrives at wrong conclusions about the roles of Collembola in soil forming processes.

I am not implying that all species of Collembola play a role in soil formation. The same situation occurs in almost all groups of soil arthropods, and we must always distinguish ecological groups.

As already mentioned, the Collembola have a leading role in forming the soil microstructure in some arctic, alpine and weakly developed soils. Sometime the whole soil profile of these soils is formed primarily by collembolan droppings (Fig. 14). In more developed soils Collembola take part in disintegration of leaf litter (Fig. 6) and in secondary disintegration of macro- and



Fig. 9. *Hypochtonius* sp. (Oribatei), v-ventriculus; p-peritrophic membrane with a ball of food particles inside. Semi-thin section prepared by Smrž. Fig. 10. *Abies alba* needles disintegrated inside by phthiracarid mites (Oribatei). Their pellets are of typical shape (o). Fig. 11. *Bourletiella lutea* (Collembola) feeding on living plant tissues does not contribute to the soil microstructures.



Fig. 12. *Tomocerus minor*, an epigeic species of Collembola.—Feeding on the leaves in the L-layer contributes to the soil microstructures by its small cylindrical pellets (a group of them on the right side). Fig. 13. *Orchesella cincta* (Collembola) takes part in leaf litter disintegration. Fig. 14. Pellets of Collembola predominate in some alpine soil types. Schneetälchen rendzina, West Tatra mountains.

megafauna droppings (Fig. 8). The small collembolan pellets can be found in lumbricid channels, as well as inside their large, spongy excrements in which the *Collembola* bite narrow hollows and channels. Collembolan droppings are often confused with pellets of enchytraeids.

Droppings of Enchytraeidae

The enchytraeids are intermediate in body length between the soil mesofauna and macrofauna. In the size of their excrements, they are close to the mesofauna. The droppings are described in many papers (e.g., Zachariae, 1964; Babel, 1968; Rusek, 1975). The pellets of some enchytraeid species resemble those of *Collembola*; in other species, they differ distinctly from the collembolan ones in their shape, size, and arrangement and location in the soil profile. They are the leading microstructural components in some soils (Babel, 1968). In the lower L-layer, the enchytraeid pellets are often in two parallel rows, forming channels between the leaves (Zachariae, 1964). In the F- and H-horizons enchytraeids are secondary decomposers of the larger excrements of soil macrofauna (Fig. 8). They make narrow channels in the large, spongy earthworm excrements (Zachariae, 1964).

The enchytraeid droppings are 120–200 μm long, of extremely irregular shape, and with irregular surface. They contain mineral particles and pieces of plant tissues and many are divided into primary components (pellets of microarthropods, plant and mineral particles). In the deeper soil horizons most contain mineral particles larger than the collembolan pellets, and the collembolan pellets are smaller than are those of the enchytraeids.

Droppings of Diptera, Coleoptera and larvae of other insects

Larvae of Diptera belong partly to the soil mesofauna (*Lycoridae*, *Mycetophilidae*, *Chironomidae* etc.), and partly to the macrofauna (*Tipulidae*, *Bibionidae*, etc.). Most form spherical, cylindrical or spindle-like droppings belonging to the moder humus form. They contain large pieces of plant tissues mixed sparsely with mineral particles, which may sometimes be missing. Their length ranges from 100 μm to 1 mm (*Bibionidae*, *Lycoridae*, *Mycoridae*, *Mycetophilidae*, and even more (*Tipulidae*). The droppings of *Bibionidae* are well described by Szabo *et al.* (1967). They contain leaf residues, some algal filaments, structureless organic substances and mineral particles, and they reach 0.3 to 0.4 mm in diameter and are up to 1 mm long. The droppings of *Tipulidae* larvae (Fig. 15) are egg-shaped and contain large pieces of plant material mixed in many cases with large mineral particles. Their surface is covered by a peritrophic membrane. They are concentrated in the litter layer and some species also are in the uppermost H-horizon. The droppings of litter feeding mycetophilid larvae are concentrated in the L-layer. They are spherical and contain small pieces of leaf tissues, 70–200 μm in diameter and are not very stable.

Also some larvae of Coleoptera contribute to the soil microstructures. Droppings of some groups are spherical, some more than 5 mm in diameter (*Melolontha* spp.); others resemble large droppings of Enchytraeidae, e.g., those of *Dryops rudolfi* (Figs. 16, 17). The droppings of the last species are an important part of the microstructure in the temporarily inundated soils in South Moravia (Rusek, 1973, 1984).

Bal (1970) described droppings of *Adela* sp. caterpillars disintegrating coniferous needles. They are cylindrical, solid, often contracted in the middle, with pieces of plant tissues. Their size reaches 510 x 260 μm and they are deposited in small groups.

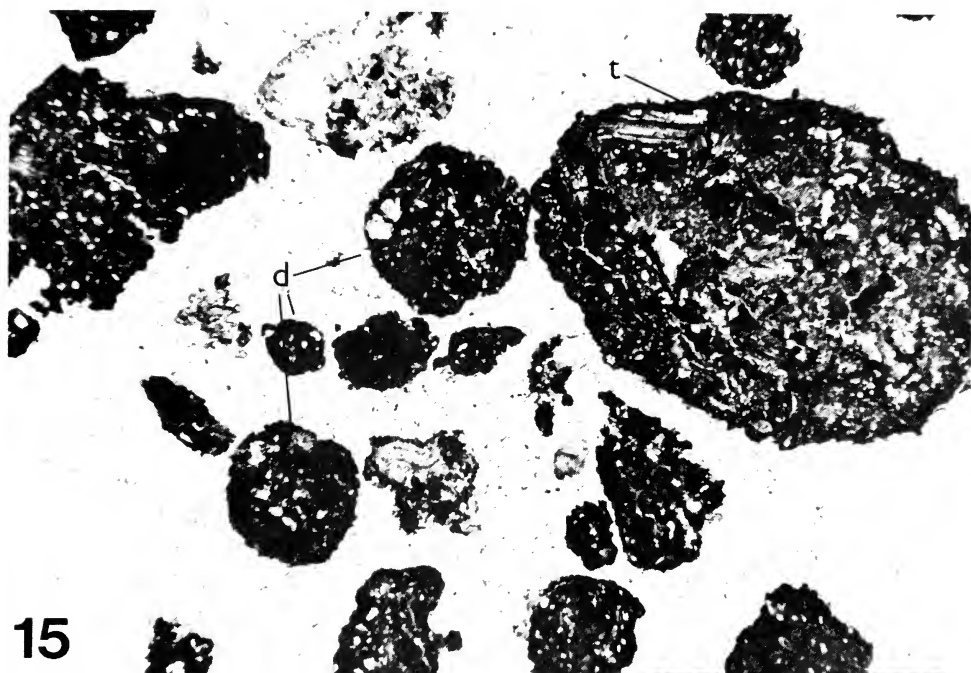


Fig. 15. Diplopod (d) and tipulid (t) larvae pellets in a moder rendzina in Bohemian Karst. Fig. 16. *Dryops rudolfi* larva (Coleoptera: Dryopidae) from a periodically flooded swampy meadow in south Moravia. Gut filled with black particles of dead organic matter and mineral particles.

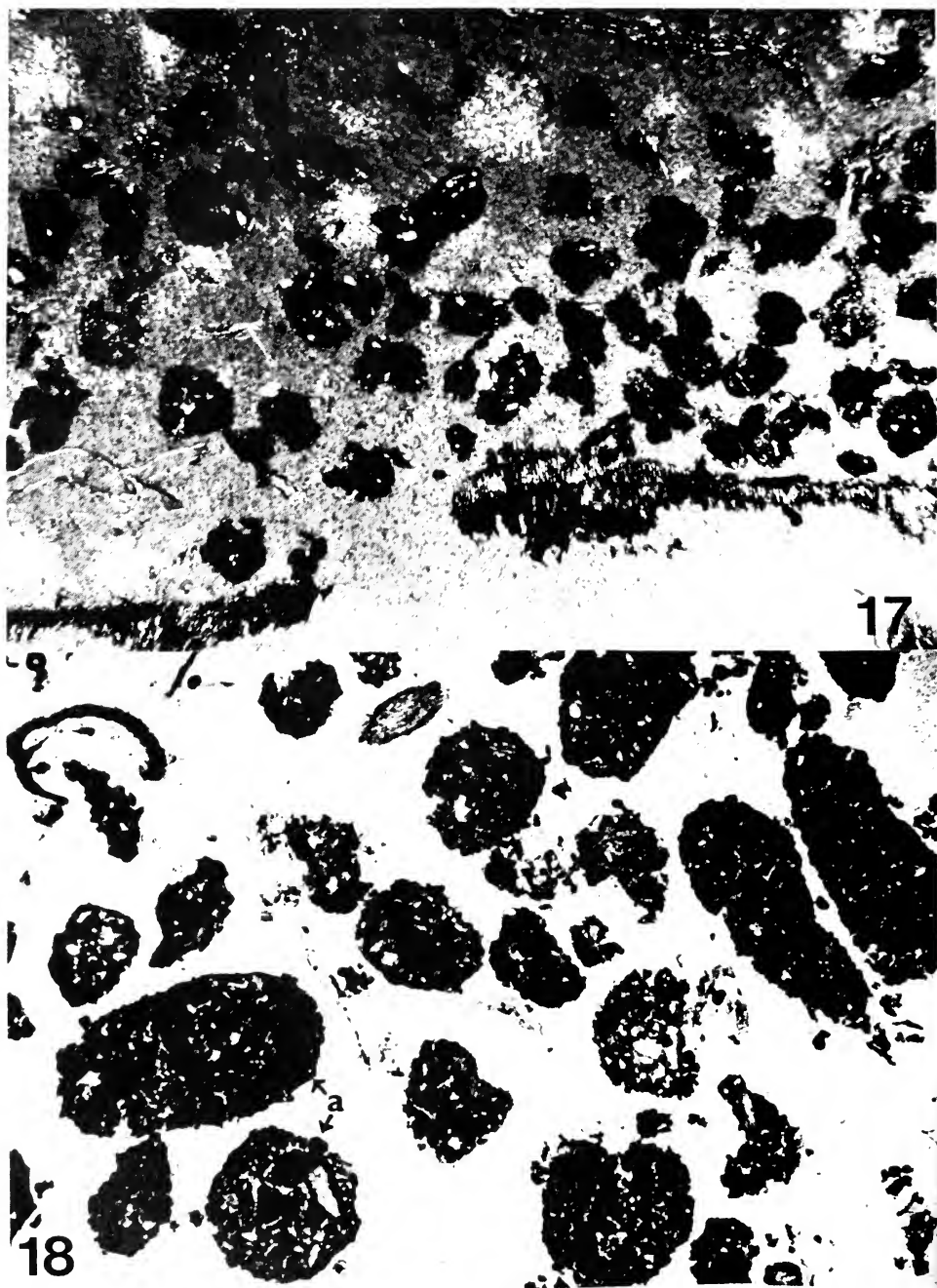


Fig. 17. Droppings of *Dryops rudolfi* larvae with residue of disintegrated leaves of *Glyceria maxima* in L-layer. Fig. 18. Droppings of diplopods (a) in a mull-like moder rendzina in Bohemian Karst.

Droppings of Diplopoda and Isopoda

The droppings of litter-consuming diplopods are characteristic microstructural elements in many soil types. They are, for example, the dominant droppings in moder rendzina and in the upper part of mull-like rendzina (Kubíková and Rusek, 1976). The diplopod droppings range in size from 0.5 to 4 mm. Many contain large pieces of litter fragments, droppings of smaller soil animals and many also a great quantity of mineral particles. The internal structure is not very compact (Fig. 18). In most species, the droppings are covered with a peritrophic membrane. The droppings of large julids and glomerids are egg-shaped or spherical; those of small julids are elongate (Babel, 1975).

Droppings of isopods, which also consume litter are very similar. These droppings are relatively rare in thin sections of soil due to the special ecological requirements of most isopod species. The animals may be slightly more abundant in very small specific areas. The size and internal structure of their pellets is almost the same as in diplopods. They are cylindrical and some have a longitudinal cleft.

Droppings of Lumbricidae

The microstructures of lumbricid droppings are well known, and they are described in almost all contributions dealing with the role of soil fauna in the formation of soil microstructure (e.g., Kubiena, 1958; Zachariae, 1965; Babel, 1975). The structure, size and internal composition of lumbricid droppings depend on the ecological group which produces them. The epigeic forms produce microstructures belonging to the moder form of humus, the endogeic and anecic ones produce mull-like or mull excrements. The epigeic group usually produces cylindrical or irregular droppings containing plant material of different stages of degradation (brown to black in colour) mixed with some mineral particles (*Dendrobaena rubida*, *Eisenia foetida*, *Eisenia lucens*, etc.) (Fig. 6). The droppings of endogeic and anecic groups are spongy, with very small pieces of organic matter well mixed with a great quantity of mineral particles of variable size (Fig. 7). Most of these droppings are usually subsequently disintegrated by the mesofauna (Fig. 8). They may occupy the whole humus horizon and the upper parts of the mineral horizon, and within lumbricid channels they may extend deep into the C-horizon.

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SOME IMPACTS OF FUNGAL-FAUNAL INTERACTIONS IN SOIL

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Soils support complex, heterogeneously distributed communities of soil animals and soil microorganisms. While accurate methods are available for comprehensive qualitative studies of the diverse taxa of the soil fauna, such work is impossible for the soil microflora (in spite of the fact that much attention has been given to microbiological methodology). Nevertheless, available information (e.g., Satchell, 1971; Persson *et al.*, 1980) indicates that, at least in temperate ecosystems, the microflora (and fungi in particular) have much greater biomass and contribution to total respiratory metabolism (Reichle, 1977) in soil and litter than do the fauna.

Decomposer activity of the microflora in organic debris is determined by such factors as temperature, moisture regimes, resource quality and quantity, and by the inoculum potential and competitive abilities of the decomposer organisms (Visser, 1985). But activities of the litter fauna (litter grazers, microbivores, detritivores and predators) must be superimposed on those of the microflora and affect:

1. the community structure of the litter microflora.
2. the patterns of decomposition of organic matter.
3. the retention and release of nutrients (attendant on organic matter decomposition).

These effects are brought about in three major ways (Visser, 1985) i.e.

1. by comminution, mixing and channelling of litter and soil: this not only causes increased surface area for microbial colonization but also can lead to a decrease in species richness of fungi and a diversion of their "successional patterns."
2. grazing on the microflora: while many studies have indicated that faunal grazing removes only a small proportion of the microbial biomass, selective grazing (when it occurs) can affect microbial community structure and, possibly, organic matter decomposition rates. Grazing also affects nutrient cycling a) by "tying up" nutrients in this faunal biomass, and, b) by accelerating nutrient release into the soil solution.
3. dispersal of microbial propagules: apart from very specific fungal-faunal relationships (Ingold, 1971) fauna carry (superficially and in their faeces) the cells and spores of a wide variety of saprophytic microbes into new substrates. Therefore microbial community structure and hence organic matter decomposition rates may be substantially affected.

Faunal activities, particularly organic matter comminution, channelling into organic substrata and soil, and defaecation can significantly affect the micromorphology of the organic layers of soils and, in some cases, the upper mineral horizon e.g., by reduction of particle size of organic matter (with consequent effects on pore volume), by channel formation, and by the

movement of organic matter into the mineral horizons.

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EARTHWORMS IN SOIL FORMATION, STRUCTURE AND FERTILITY

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ABSTRACT

The importance of earthworm activity has been recognized since ancient times and their role in pedogenesis and soil fertility has been studied since the late 1800's. Earthworms contribute to soil structure and formation through burrowing, comminution of organic matter and by formation of aggregates. Earthworm guts are important sites of microbial action whereby nutrients are made available to plants. Earthworm burrows are conspicuous aspects of soil structure and contribute to soil aeration and drainage. Earthworm populations can be extremely dense in soils with abundant organic matter, although species diversity of earthworm assemblages is relatively low. Empirical data suggest that introduction of earthworms can improve impoverished soils. However, important information about taxonomy, distribution and biology of North American species is lacking. Few ecological studies have examined relationships between earthworms and other organisms in the soil.

RÉSUMÉ

L'importance de l'activité des vers de terre est connue depuis les temps anciens, et leur rôle dans la pédogénèse et la formation des sols est le sujet d'études depuis la fin du XIX^{ème} siècle. Les vers de terre contribuent à la structure et à la formation des sols en fouissant, en pulvérisant la matière organique et en formant des agrégats. Le tube digestif des vers de terre est le site important d'une action microbienne par laquelle les nutriments sont libérés des tissus végétaux. Les galeries de vers forment un aspect frappant de la structure du sol et contribuent à son aération et à son drainage. Les populations de vers peuvent être extrêmement denses dans les sols riches en matières organiques, mais la diversité des espèces en est relativement faible. Des données empiriques suggèrent que l'introduction de vers de terre peut améliorer les sols appauvris. On manque cependant d'informations essentielles sur la taxonomie, la répartition géographique et l'histoire naturelle des espèces de vers nord-américaines. Peu d'études écologiques ont examinées les rapports entre les vers de terre et les autres organismes du sol.

INTRODUCTION

The great importance of the soil biota in soil pedogenesis and in the maintenance of structure and fertility is not always fully appreciated by soil scientists. Earthworms are probably one of the most important components of the soil biota in terms of soil formation. Although they are not numerically dominant, their large size makes them one of the major contributors to animal biomass, and their activities are such that they are extremely important in maintaining soil fertility in a variety of ways.

Aristotle was the first to draw attention to their role in turning over the soil and he aptly called them "the intestines of the earth". However, it was not until the late 1800's that Charles Darwin, in his definitive work, "The Formation of Vegetable Mould Through the Action of Worms", defined the extreme importance of earthworms in breakdown of dead plant and animal matter that reaches soil and in the continued maintenance of soil structure, aeration

drainage and fertility. His views were supported and expanded subsequently by other contemporary scientists such as Muller (1878) and Urquhart (1887) and many others.

Earthworms belong to the Order Oligochaeta which contains about 3,000 species, although considerable numbers of these are aquatic in habit, and there is considerable controversy on their systematics. They are found in most parts of the world, except those with extreme climates, such as deserts and areas under constant snow and ice. Some species of earthworms, particularly those belonging to the Lumbricidae, are extremely widely distributed ('peregrine') and often, these species when introduced to new areas, become dominant over the endemic species; this situation probably applies to parts of the northern United States and Canada, particularly those close to major waterways. However, the endemic earthworm fauna of North America has not been well studied. Endemic species include those in the Acanthodrilidae with its most abundant genus *Diplocardia*, members of the Sparganophilidae and species in the Megascolecidae of which the most common genus is *Pheretima*.

EARTHWORMS AND SOIL

Soil Formation

Earthworms are extremely important in soil formation, principally through their activities in consuming organic matter, fragmenting it and mixing it intimately with mineral particles to form *aggregates*. During their feeding, earthworms greatly promote microbial activity which in turn also accelerates the breakdown of organic matter. Different species of worms do not all affect soil formation in the same way. Some species consume mainly inorganic fractions of soil, whereas others feed almost exclusively on decaying organic matter. They can deposit their feces as casts either on the soil surface or leave them in their burrows, depending on the species concerned, but all species contribute in different degrees to the comminution and mixing of the organic and inorganic components of soil, and decrease the size of not only organic but also mineral particles (Joshi and Kelkan, 1952; Shrikhande and Pathak, 1951). During passage through the earthworm gut, the different kinds of particles become mixed intimately and form aggregates, which improve both the drainage and moisture-loading capacity of the soil. These aggregates are usually very stable and improve many of the desirable characteristics of soils. There have been various suggestions as to the possible ways in which earthworms form aggregates, such as by production of gums (Swaby, 1950), or calcium humate (Meyer, 1943), by plant residues (Ponomareva, 1953) or by means of polysaccharide molecules (Parle, 1963). Various authors have estimated that up to 50% of the aggregates in the surface layers of soil are formed by earthworms (Kubiena, 1953).

Earthworms move large amounts of soil from the deeper strata up to the surface. The amounts moved in this way range from 2 - 250 tons per ha per annum, equivalent to bringing a layer of soil between 1 mm and 5 cm thick to the surface every year, creating a stone-free layer on the soil surface. Earthworms also affect soil structure in other ways. Some species make 'permanent' burrows, whereas others move randomly through soil leaving cracks and crevices of different sizes. Both sorts of burrows are important in maintaining both *soil aeration* and *drainage*. Moreover, earthworm burrows are usually lined with a protein-based mucus, which helps to stabilize these cavities, and many of the species with permanent burrows cast their feces around the lining of their burrows, the cast material usually containing more plant nutrients in a readily available form than the surrounding soil. There is good evidence that earthworm activity increases the *porosity* and *air to soil volume* (Wollny, 1890; Hopp, 1974; Edwards and Lofty, 1977). Burrows are also important in improving *soil drainage*, particularly

since those of some species, such as *Lumbricus terrestris* L. penetrate deep into soil (Edwards and Lofty, 1978, 1982) and can even pass through layers of clay. The burrows and pores also increase the *infiltration rate* greatly (Slater and Hopp, 1947; Teotia *et al.*, 1950; Carter *et al.*, 1982), and there are numerous reports of water penetrating the surface soil between two and ten times faster when earthworms were present than when they were not (Stockdill, 1966; Wilkinson, 1975; Tisdall, 1978). This effect on infiltration can be of two kinds; firstly, the presence of large surface-opening holes which are not usually taken into account by soil scientists when conventional models of infiltration are developed (Edwards *et al.*, 1979), and secondly, the crevices also created by earthworms, but which are much smaller, not only increase infiltration but also aid in water retention.

Finally, earthworm activity makes a significant contribution to soil *aeration* (Stockli, 1928; Kretschmar, 1978), by creating channels, particularly in heavy soils which allow air to penetrate into the deeper layers of soil, minimizing the incidence of anaerobic layers.

Organic matter breakdown and incorporation into soil

Although all species of earthworms contribute to the breakdown of plant-derived organic matter, they differ in the ways in which they breakdown organic matter. Their activities can be of three kinds, each associated with a different group of species. Some species are limited mainly to the plant litter layer on the soil surface, decaying organic matter or wood, and seldom penetrate soil more than superficially. The main role of these species seems to be comminution of the organic matter into fine particles which facilitates microbial activity. Other species live just below the soil surface most of the year, except when very cold or very dry, do not have permanent burrows and ingest both organic matter and inorganic materials. These species produce organically enriched soil materials in the form of casts, which they deposit either randomly in the surface layers of soil or as distinct casts on the soil surface. Finally, there are the truly soil-inhabiting species which have permanent burrows that penetrate deep into the soil. These species feed primarily on organic matter but also ingest considerable quantities of inorganic materials and mix these thoroughly through the soil profile. These latter species are of primary importance in pedogenesis. All species depend on consuming organic matter in some form and play an important role in the final stage of organic matter decomposition, which is humification into complex amorphous colloids containing phenolic materials, probably by promoting microbial activity.

There is little doubt that in many habitats, earthworms are the key organisms in the breakdown of plant organic matter. Populations of earthworms usually expand in relation to the availability of organic matter, and in many temperate and even tropical forests, it seems that earthworms have the capacity to consume the total annual litter fall. Such a total turnover has been calculated for an English mixed woodland (Satchell, 1967), an English apple orchard (Raw, 1962), a tropical forest in Nigeria (Madge, 1965), an oak forest in Japan (Sugi and Tanaka, 1978) and it seems likely that similar calculations would be valid for other sites (Edwards and Lofty, 1977).

During feeding by earthworms, the carbon:nitrogen ratio in the organic matter falls progressively and, moreover, the nitrogen is converted into the ammonium or nitrate form. At the same time the other nutrients, P and K, are converted into a form available to plants. Soils that have poor populations of earthworms often develop a mor structure with a mat of undecomposed organic matter at the soil surface (Kubiśna, 1953); this can also occur in grassland and is common on poor upland grasslands in temperate countries and in New

Zealand in areas where earthworms have not yet been introduced (Stockdill, 1966).

ECOLOGICAL ASPECTS OF EARTHWORMS

Abundance and Diversity

Populations of earthworms vary greatly both in terms of numbers or biomass and diversity. Populations range from only a few per square meter to more than 1,000 per square meter. Numbers depend on a wide range of factors, including soil type, pH, moisture-loading capacity of the soil, rainfall and ambient temperatures, but, most importantly, to the availability of organic matter. Populations in cultivated land seldom exceed 100 per square meter, or 400 per square meter in grassland, the larger populations usually being found in woodlands where the availability of organic matter is seldom limiting, and occasionally numbers as high as 2,000 per square meter have been recorded, although few earthworms occur in the more acid soils under coniferous forests. Usually, the largest populations are of lumbricid earthworms which seem to be able to survive adverse conditions much better than species belonging to the other families.

The diversity of species of earthworms varies greatly and there tend to be species associations in different soil types and habitats. The associations of species of lumbricids in temperate countries tend to be less diverse than those from other families in warmer latitudes. However, even in the most complex system, the diversity of species does not seem to be very great, rarely exceeds 10 and commonly, there are only 3-5 species. There is some evidence that species that fill the same ecological niche do not normally occur in the same degree of abundance at a particular site (Edwards and Lofty, 1982).

Needs for earthworm research

In view of the great importance of earthworms in soil formation and maintenance of soil fertility, although the numbers of publications on earthworm biology and ecology is increasing rapidly, there still seems an urgent need for greatly expanded research, particularly on some aspects of earthworm activity.

We still have inadequate knowledge of the basic biology and ecology of even the more common species of lumbricids. Very few studies have addressed the problems of the detailed interrelationships between earthworms, micro-organisms and decaying organic matter and its incorporation into soil. There is good empirical evidence that introduction of earthworms together with organic matter, into impoverished soil with addition of organic matter and adjustment of pH, can increase their fertility greatly, but we have little knowledge of the mechanism of such increases or even the best ways of introducing earthworms.

Most important is the world-wide lack of knowledge of the distribution of earthworms and populations of the different species. Until we know more of the fundamental biology and ecology and the activities of the many different species and their role in maintaining soil structure and fertility, it is impossible to assess their potential role in soil improvement. These problems are particularly acute in North America where earthworm specialists are rare and research extremely sparse.

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ASPECTS OF THE BIOLOGY AND SYSTEMATICS OF SOIL ARACHNIDS, PARTICULARLY SAPROPHAGOUS AND MYCOPHAGOUS MITES

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ABSTRACT

Among members of the class Arachnida, the saprophagous and mycophagous mites are the most diverse and abundant in soil systems, and have the greatest effects on soil structure and fertility. In most soils, the oribatid mites are the only arachnids which directly affect soil structure; they ingest particulate food and produce discrete fecal pellets, the possible functions of which are discussed. Current research is finding an active gut microflora in both saprophagous and mycophagous oribatid mites. For those species in which the diet varies seasonally, it is suggested that the gut microflora also changes, reflecting the new substrates. Particulate-mycophagy is a very old feeding habit, and was probably the ancestral one of the earliest known (Devonian) oribatid mites. Saprophagy may have originally developed as a mechanism for obtaining non-surface microbial tissue or exometabolites from decaying higher plant materials. The use of the plant structural parts as food may have been made possible by changes in gut microflora. The mite suborder Prostigmata also contains important soil mycophages, but these feed intracellularly and contribute little to soil structure. They are more "r-selected" than oribatid mites and may show numerical responses to temporary increases in food supply.

The descriptive taxonomy and systematics of North American saprophagous and mycophagous soil mites are in a poor state. Currently no "user-friendly" monographs are available for any major group, and higher classifications based on the methodology of phylogenetic systematics are only beginning to be proposed.

RÉSUMÉ

Parmi les membres de la classe des Arachnides qui vivent dans les sols, les mites saprophages et mycophages sont les plus divers et les plus abondants, et sont ceux dont les effets sur la structure et la fertilité des sols sont les plus marqués. Dans la plupart des sols, les mites oribatides sont les seuls arachnides qui affectent directement la structure du sol; elles ingèrent des aliments particulaires et excrètent des boulettes fécales, dont les fonctions possibles sont examinées. Les recherches actuelles révèlent une flore active du tube digestif chez les mites oribatides autant saprophages que mycophages. Chez les espèces dont la diète varie saisonnièrement, il est possible que la microflore du tube digestif change aussi, reflétant ainsi les divers substrats. La mycophagie particulaire est une très vieille habitude alimentaire qui remonte probablement aux plus anciennes mites oribatides connues (du Dévonien). La saprophagie pourrait à l'origine être apparue comme un mécanisme permettant d'obtenir des couches sous-jacentes de tissus microbiens ou des exométabolites provenant de plantes supérieures en décomposition. L'utilisation de parties structurales des plantes comme nourriture a pu être rendue possible par des changements dans la microflore du tube digestif. Les mites du sous-ordre Prostigmata incluent aussi d'importants mycophages du sol, mais ceux-ci se nourrissent intra-cellulairement et ne contribuent à peu près pas à la structure des sols. Elles sont davantage soumises à la r-sélection que les mites

oribatides et peuvent voir leur nombre augmenter à la suite d'un accroissement temporaire de la quantité de nourriture disponible.

La taxonomie descriptive et la systématique des mites nord-américaines saprophages et mycophages des sol est dans un état lamentable. Présentement il n'existe aucune monographie d'utilisation facile pour aucun des groupes majeurs, et des classifications supérieures basées sur les méthodes de la systématique phylogénétique commencent à peine à faire leur apparition.

INTRODUCTION

The subject of biology and systematics of the Class Arachnida is large even if one's attention is restricted to soil dwellers. Representatives of this class usually dominate the arthropod fauna of soils; numbers in the hundreds of thousands per surface m^2 are common (Petersen, 1981a). The soil arachnid fauna can be conceptualized and categorized from many viewpoints, but the one used here is that of function, particularly predation, saprophagy and mycophagy.

Predation is the most ancient and general feeding strategy of arachnids and predaceous species abound in soil and litter. Various groups of cursorial spiders constitute a major fraction of the larger (length > 1 cm) predaceous soil arthropods; pseudoscorpions and harvestmen, along with other spider groups, are intermediate (1 mm - 1 cm) in size. By far the greatest diversity of small arthropod predators in most soil systems is contributed by representatives of two suborders of mites, the Mesostigmata (temperate region soil dwellers are mostly predators) and the Prostigmata (in part). The latter group also includes taxa which are external parasites of other arthropods. Little will be said here regarding these predators and parasites, since their influence on physical and chemical attributes of soil is at best indirect, through their regulatory interactions with other soil animals. This is not meant to infer that they are unimportant to the proper functioning of soil systems; we simply have little empirical information. Progress has been made in understanding the role of spider predation in agroecosystems (Riechert, 1984), where they are generalist background regulators of insect populations, but their role in soil/litter systems is virtually untested, except for the work of Clarke and Grant (1968) and Kajak and Jakubczyk (1977), who demonstrated higher densities of centipedes and saprophages such as collembolans after removal or exclusion of spiders and other large predators. Even the detailed study by Moulder and Reichle (1972) on the significance of spider predation in the forest floor fell short due to lack of information on prey dynamics. The role of predation in regulating soil arthropod and nematode (see Karg, 1983) densities remains, for the most part, unknown. An exception is the important role of predaceous Tydeidae (Prostigmata) in regulating bacteriophagous nematode populations in desert soils (*e.g.*, Whitford and Santos, 1980).

It is the arachnid groups generally considered to be saprophagous and mycophagous (fungivorous) which are of greatest interest from the standpoint of soil structure and fertility, and these will be stressed in the discussions which follow. Saprophages, those feeding directly on decomposing leafy or woody vegetation (macrophytophages of Schuster, 1956) have the greater significance in producing structure in organic horizons, particularly by comminution activities and production of feces. Among the Arachnida, mites of the suborder Oribatida (Cryptostigmata) perform this function on a scale which is small in size, but not necessarily in overall effect. Fungivorous mites abound in soils, and along with Collembola form the dominant mycophages in most terrestrial ecosystems (Seastedt, 1984). Two general fungal-feeding strategies are apparent: the fungivorous oribatid mites are particulate feeders, and produce discrete fecal pellets which contribute to soil structure. The fungivorous prostigmatid (trombidiform) mites feed intracellularly by means of styletiform chelicerae and contribute

little to soil fabric.

Due to the scope of the topic, available, this paper cannot be considered a complete review of current problems in arachnid biology and systematics. Only saprophagous and microphytophagous (bacterial and fungal feeders) arachnids will be dealt with in any detail. In particular, the oribatid mites are emphasized, for several reasons: 1) they are usually the dominant arachnid group in terms of numbers and biomass (Petersen, 1982a, 1982b); 2) they are apparently the most important group of soil arachnids from the standpoint of direct and indirect effects on the formation and maintenance of soil structure; 3) they are the best known biologically, even if "best" is not very good; and 4) they are the soil animals with which I am most familiar. Little will be said of the mite suborder Astigmata; their occurrence in soils is sporadic and their overall importance is likely to slight (Luxton, 1981a; see O'Connor, 1982 and Woodring, 1963). Even with these restrictions my comments will be selective. From the standpoint of biology, I will deal particularly with certain aspects of nutrition, followed by brief remarks on population dynamics, and then review how the feeding activity of these animals affects soil structure and fertility. Lastly, I will offer some comments on systematics of soil arachnids, again with emphasis on non-predators.

BIOLOGY

Some Aspects of Oribatid Mite Nutrition

The diet and method of feeding of saprophagous and mycophagous soil mites greatly influences the effect they have on soil structure and fertility. Such information was rather scattered and anecdotal before Schuster's (1956) classic paper, which described feeding habits of a wide variety of European oribatid mite. Since that time numerous authors have approached the subject, generally using one or more of three methods: laboratory food preference tests, gut content analysis of field-collected specimens, or the study of gut enzyme complements [see studies and reviews by Wallwork (1967), Lebrun (1971), Luxton (1972), Pande and Berthet (1973), Behan and Hill (1978), Behan-Pelletier and Hill (1983), and especially Harding and Stuttard(1974)].

Each of these techniques has associated problems. Laboratory preference tests are limited by our ability to discern and supply the food items available in nature and to keep other, often unknown, variables within preference, or at least tolerance, ranges of the mites being tested. Simple choice experiments rarely fail to demonstrate preferences, yet these preferred foods may not, in some circumstances, be the ones chosen in nature, even if they are available (Mitchell and Parkinson, 1976). Also, even heavy feeding on a given food does not mean that reproductive or developmental success is necessarily possible (Luxton, 1972; Saichuae *et al.*, 1972; Mitchell and Parkinson, 1976; Stefaniak and Senniczak, 1981).

Gut content analyses have the disadvantage that less easily digestible materials will be overestimated in dietary quantification (Behan-Pelletier and Hill, 1983). In some situations, readily digestible materials may be supplying most of an animal's requirements, yet rarely be seen in the gut by conventional methods. For example, it is unknown to what extent oribatid mites are predatory or necrophagous. Muraoka and Ishibashi (1976) and Rockett (1980) have demonstrated active feeding on living and dead nematodes by brachypyline oribatid mites and the importance of this in nature needs investigation. Stefaniak and Seniczak (1981) found that cannibalism could occur in oribatid mites in association with poor nutrition, and Behan-Pelletier and Hill (1983) found unusually high quantities of small animal remains in guts of acid-bog dwelling oribatid mites. They also suggested that the presence of such dietary

components might be related to the overall poor nutrient content of other available foods. The role of bacteria or other Monera, scraped from soil substrates, as food for oribatid mites is virtually unknown. Luxton (1972) demonstrated attractiveness of bacteria to some species, and Behan-Pelletier and Hill (1983) found high percentages of Monera in some oribatid guts, but whether they are truly food sources, or function as symbiotic sources of enzymes necessary to complement the mites' endogenous enzyme system, or both, remains to be elucidated (see below).

Studies of gut enzymes (Luxton, 1972; Zinkler, 1971, 1972) have been enlightening, but they are typically done on whole-body homogenates and give no information on the origin of any given enzyme. Luxton (1972, 1979) suggested that enzyme complements of oribatid mites correspond to the exhibited feeding habits. Species which are principally saprophagous (in particular the *xylophagous*, family Phthiracaridae) possess enzymes capable of hydrolyzing structural carbohydrates of higher plants (e.g., cellulase, xylanase, pectinase), whereas those ingesting primarily fungal tissue can hydrolyze the fungal storage sugar trehalose and perhaps chitin, which is found in hyphal walls. Only panphytophagous (unspecialized) species possess both enzyme systems. Two other authors (Zinkler, 1972; Dinsdale, 1974), however, failed to find a cellulase in phthiracarid mites. There is mounting evidence that many carbohydrase enzymes, including cellulase and chitinase, are produced by a diverse and very active microflora (Seniczak and Stefaniak, 1978; Stefaniak and Seniczak, 1976, 1981). These studies indicate that the composition of the gut microflora in both panphytophages and mycophages (and the enzymes produced) depends on the food ingested, and is not identical to the microflora of the surrounding environment. Their floral lists indicate that a subtraction process occurs. Those microorganisms capable of continued (or enhanced?) enzymatic production in the gut may be those which are resistant to digestion. Dinsdale (1974) has demonstrated that in *Phthiracarus* sp. (which had few demonstrated gut microflora) enzymes acting on the glucosidic bonds of simple storage carbohydrates were closely associated with the gut mucosa, and protein digestion appeared to be intracellular, with evidence of pinocytosis. One can speculate that these enzymes are endogenous, and that all enzymes acting on structural polysaccharides which are found in oribatid mite guts are of microbial origin, as they apparently are in all other arthropods which possess them.

It has been known for many years that saprophagous oribatid mites will only eat material if it has been previously attacked by microorganisms (see Harding and Stuttard, 1974), but the earlier consensus view was that the microbial tissue itself, or exometabolites from its decomposition activities, provided the only energy source. The finding of active gut microflora in saprophagous groups is not surprising, but it is somewhat surprising that fungivorous mites may have a strong dependence on gut microflora.

The implications and questions raised by Stefaniak and Seniczak's work are important ones and relate to the ability of soil mites to adjust to forced or opportunistic changes in diet. There is growing evidence (e.g., Anderson, 1975; Swift, Heal and Anderson, 1979) that in some soils many or most oribatid mites do not adhere strictly to saprophagy or mycophagy throughout the year. Feeding is catholic, and gut contents of a given species can vary with site and season. At times even those species normally associated with strict xylophagy (Phthiracaridae) can be fungivorous, and those with chelicerae seemingly specialized for mycophagy, such as *Eupelops*, can be saprophagous (Wallwork, 1967; Anderson, 1975; Behan-Pelletier and Hill, 1983). Anderson (1975), working in a British deciduous forest, considered mycophagy to be the dominant feeding activity by oribatid mites soon after leaf fall in autumn. Within a rapidly

degraded litter layer, fungi were less easily available during the following season, and feeding activity changed to mixed mycophagy/saprophagy and then to saprophagy prior to the following leaf-fall. Such patterns were apparent even within populations of a given species.

A seemingly conflicting pattern was found, however, in a Canadian aspen forest soil (Mitchell and Parkinson, 1976) where the litter layer was more stable. The dominant taxa were primarily fungivorous and there were one or two seasonal peaks in feeding rate related to leaf-fall. Perhaps most interesting was the fact that overall feeding rate was related to general microbial activity, and opportunistic switching to saprophagy apparently did not occur at this site. Nor did Behan-Pelletier and Hill (1983) find seasonal patterns in diet composition during a six-month study of feeding by oribatid mites in an Irish acid peat bog, other than opportunistic use of pollen. For the most part, species were panphytophagous. It seems that the existence of seasonal patterns in oribatid mite feeding depends on site characteristics, especially the rate of early decomposition. Where major diet changes do occur, as in Anderson's (1975) site, one can speculate that they are made possible by passive access to a rich variety of symbiotic microflora ingested with the food. Different bacterial floras (and their respective enzyme complements) may preferentially develop in the gut during the part of the season when the appropriate food enters the diet. Stefaniak and Seniczak (1976, 1981) have demonstrated such a relationship between food type and the composition of the gut microflora under both saprophagous and mycophagous feeding regimes. Perhaps in less active sites, such as that studied by Mitchell, changes in available microflora are insufficient to necessitate a switch, or perhaps climatic or other factors intervene when fungal availability is low, resulting in lower ingestion rates rather than dietary changes. The ability of any oribatid mites to change diet has been suggested to be adaptive from the standpoint of increasing survival probability in variable or different environments (Wallwork, 1958; Luxton, 1972), but it is interesting that the two most widely distributed (both geographically and ecologically) and successful species known, *Tectocephus velatus* (Michael) and *Oppeilla nova* (Oudemans), are apparently strictly mycophagous.

Saprophagy and Mycophagy in Other Soil Mite Groups

Compared to oribatid mites, little is known of the feeding biology of other mycophagous or saprophagous mite taxa. Members of the Uropodina (belonging to the predominantly predaceous suborder Mesostigmata) exhibit these feeding habits, (Krantz, 1978), but they do not constitute an important fraction of the soil fauna in most areas of North America; in the tropics they are much more abundant, often outnumbering oribatid mites. Like their predaceous relatives, they are predominantly liquid-feeders (Karg, 1963; Ahtias-Binche, 1977, 1981) so their influence on soil structure is probably minimal.

A different type of mycophagy is exhibited by some members of the suborder Prostigmata. The apparent majority of fungal-feeding soil Prostigmata to the families Eupodidae, Tydeidae, Tarsonemidae, Scutacaridae, and Phgmephoridae (Evans *et al.*, 1961; Karg, 1963; Krantz and Lindquist, 1979; Kethley, in press). Although present in soils of most ecosystems, these mites are especially abundant and diverse in herbaceous systems (where oribatid mites are usually not dominant) such as prairies, oil-fields and arctic sites (Petersen, 1982a) and also in desert soils (Santos *et al.*, 1978). In a study of an oil-field soil in Ohio (D. Dindal and R. Norton, unpublished) representatives of more than 100 species of Prostigmata were collected over several years, most belonging to the aforementioned families. Although there is little supporting information, their intracellular style of feeding would seem to preclude any direct impact on

soil structure, in contrast to the comminution and fecal production exhibited by particulate-feeding oribatid mites. They are not, therefore, strictly ecological equivalents, despite a common general food source. As with oribatid mites, mycophagous Prostigmata may demonstrate feeding preferences in laboratory tests (e.g., Kosir, 1975). As might be expected, no active gut microflora has been reported from these mites. Fungivory is also known in another group of mites commonly associated with the Prostigmata, a group often referred to as the "Endeostigmata" or Pachygnathoidea. At least some members of this group are considered early-derivatives of the lineage which gave rise to oribatid mites (e.g., O'Connor, 1984). Thus, it is not surprising to find particulate-mycophagy in some of these taxa, such as *Terpnacarus* (Theron, 1979) and *Grandjeanicus* (personal observation). This brings up the question of the evolutionary development of the various feeding strategies discussed to this point.

Comments on the Evolution of Mycophagy and Saprophagy in Acariform Mites

Intimate associations of arachnids and soils are as old as soils themselves (Kevan *et al.*, 1975). When terrestrial vegetation first began to flourish in Devonian times soil mites were already present, and in forms not very different from some which exist today. It is fortunate that some representatives of these ancient lineages have survived, because they give insight into not only the systematic relationships of early soil mites, but also their possible feeding habits. The earliest of the mite fossils, *Protacarus crani* from the Devonian Old Red Sandstone formation of Scotland (Hirst, 1923), is very similar to extant members of the "Endeostigmata" (Krantz, 1978), a loosely defined group which is currently thought by some (including myself) to have given rise independently to both the Prostigmata and the Oribatida-Astigmata lineages. Some extant members of the group are particulate-mycophages, as noted above. These have modified mouthparts with specialized setae (rutella) used in conjunction with the chelicerae to shear off particles as food is pulled toward the mouth (Grandjean, 1957; Theron, 1979), and appear to be part of the lineage which includes oribatid mites (also with rutella). Other "Endeostigmata," lack rutella (a few of these possibly secondarily so) and feed on spores or pierce roots to obtain nourishment (Theron, 1979). Although the mouthparts of *Protacarus* are not well described, they appear to be rather styletiform and if so, are consistent with this feeding type. The earliest known fossil oribatid mite, also of Devonian age, is apparently a member of the extant family Ctenacaridae (Shear *et al.*, 1984) which are particulate-mycophages (Grandjean, 1954; personal observation). In none of these early derivative groups (fossil or extant) is there any evidence of saprophagy, which makes Krantz and Lindquist's (1979) suggestion, that mycophagy in oribatid mites evolved from saprophagy, difficult to accept. It is far more likely that sarcoptiform mites (those with a cutting rutellum) were ancestrally mycophagous, and fed on the rich terrestrial microflora which probably existed in the primordial organic soils developing concurrently with the growth and decomposition of the earliest vascular plants.

Saprophagy was apparently derived within the oribatid mites, seemingly associated with even stronger, more robust development of the rutellum and sclerotization in general. It is reasonable to speculate that the appearance of saprophagy gave previously mycophagous mites a mechanism for ingesting non-surface microbial tissue (or easily utilized exometabolites). The use of the higher plant structural material itself, by means of a symbiotic gut microflora derived from environmental sources, may have evolved later and perhaps necessitated changes in gut chemistry to allow or promote the growth of gut bacteria and actinomycetes.

In any event, it is clear that mycophagous and saprophagous soil arachnids were not added to soils as an evolutionary "after thought", except perhaps some of the intracellular-mycophagous Prostigmata (see Krantz and Lindquist, 1979). Rather, the soil system as we know it today, with its complex patterns of energy flow and nutrient cycling, is a result of a coevolution between mites and other soil animals (the ecologically similar Collembola are equally as old), the microflora, and the developing terrestrial vegetation.

A Brief Overview of Development and Population Dynamics

Knowledge of developmental biology and population dynamics of saprophagous and mycophagous mites is essential for determining the magnitude of their relationship to soil structure and fertility. Here again, we know much more about oribatid mites than the mycophagous taxa of Prostigmata. Early estimates of developmental times for oribatids are mostly useless, since they were done with laboratory cultures at high, constant temperatures (20–30° C) and with constantly high humidity and food supply (see Lebrun, 1971; Luxton, 1981b for reviews). Consequently, grossly underestimated development and generation times were the rule. Multivoltine life histories were commonly suggested for temperate-zone oribatid mites despite the fact that annual mean temperatures in the soil may be only half those of the laboratory. The complexity and variation of natural abiotic and biotic factors make simple extrapolations impossible, in light of our knowledge of such factors as high development Q_{10} values (Lebrun and Ruymbeke, 1971), variable temperatures (Lebrun, 1977), and food quality (Saichuae *et al.*, 1972; Mitchell and Parkinson, 1976; Young and Block, 1980; Stefaniak and Seniczak, 1981) upon developmental time, survival rates, and metabolic rates of these mites.

Improved estimates have resulted from following population age-structure in the field over time (*e.g.*, Mitchell, 1977; Thomas, 1979; Luxton, 1981b, 1981c). There are difficulties with this method, however, when oviposition is not temporally circumscribed. Also, some workers have equated developmental time (egg-adult) with the more ecologically significant generation time (adult-adult). For example, Weigmann's (1979) estimate of a one-year generation time in *Platynothrus peltifer* (Koch) is possible only if eggs are laid immediately after the adult instar is reached. As Harding (1973) has shown, however, a long preoviposition period is typical for this species and what Weigmann probably observed was two principal cohorts in a population with a one year development time, but a nearly two year generation time.

The recognition of preoviposition periods and the possible presence of cohort structure suggests a need for reexamination of earlier age-structure data. It is likely that natural developmental times of oribatid mites in temperate regions (where they are generally most abundant) take a year or more, and two-year generation times are probably not uncommon. Longevity is probably relatively high in natural conditions, with iteroparity common (Mitchell, 1977; Luxton, 1981b); this may keep cohort recognition from being absolute.

Mortality factors in oribatid mite populations are poorly known. Lebrun (1969) and Mitchell (1977) suggested that mortality is concentrated in the immatures; presumably this is mostly due to predation on these soft-bodied instars and the rigors of the molting process. But adults are not immune to predation (Riha, 1951; Norton and MacNamara, 1976) and they seem to be more vulnerable to internal parasitoids (*e.g.*, Purrini, 1983 and included references). Cold-induced winter mortality may not be important (Mitchell, 1977). Adaptations to survive subfreezing temperatures have been elucidated (*e.g.*, Somme and Conradi-Larsen, 1977; Block, 1980) and include elevation of cryoprotectants (such as glycerol) in the hemolymph and the cessation of feeding to avoid the presence of ice nucleating agents in the gut. Feeding activity

during subfreezing winter temperatures may require the surpassing of a snow-thickness threshold (Aitchison, 1979).

Oribatid mites can generally be considered K-selected organisms (Mitchell, 1977). Their high diversity, low fecundity (e.g., Luxton, 1981b), increased variability in instar length as development proceeds (Lebrun, 1971; Luxton, 1981b), and high longevity coupled with iteroparity, create an overall relatively stable community, especially in forest soils. The higher oribatid mite densities often noted during winter (see Harding and Stuttard, 1974) may be artifacts of the sampling process in two different ways. Persson and Lohm (1977) found that soil compaction during sampling trapped significant numbers of microarthropods, except when the soil was frozen. Also, as reviewed by Luxton (1981b), about one-third of an oribatid mite's post-hatching development time is spent in pre-ecdysial resting stages and Lebrun (1969) has noted that this can cause substantial under-estimates of population densities calculated from desiccating-style extractors. Since molting occurs primarily during warmer months, under-estimation should especially be a problem in this period. It may be that in temperate regions the best overall estimates of population density are those obtained in late fall or early winter.

Information on population dynamics of mycophagous Prostigmata (e.g., Heterostigmata, Tydeidae, Eupodidae) is much less extensive. Information about structure of age-classes is almost non-existent, but multiple generations per year seem to be likely (Luxton, 1981d). Unlike oribatid mites, they may show numerical responses to temporary increases in food supply. Very high densities are commonly found in litter-bag studies (Crossley and Hoglund, 1962; personal observations), where the compact, moist substrate is conducive to rapid mycelial growth. At least some of these taxa (although certainly not the "Endeostigmata") are r-selected as is apparently so for some of their phytophagous aerial relatives (Krantz and Lindquist, 1979).

The Role of Saprophagous and Mycophagous Mites

The literature on the role of saprophagous and mycophagous mites and collembolans in the functioning of soil systems is full of contradictions (Cancela de Fonseca and Poinot-Balaguer, 1983), especially from the standpoint of whether or not their activities are necessary for expeditious decomposition of annual organic matter input. What is now clear is that these animals, even when abundant, use a very small amount of the annual energy input to the soil-litter system, generally less than 1% (Mitchell, 1979; Thomas, 1979; Luxton 1982a). This is principally due to their small standing crop biomass combined with a low weight-specific respiratory metabolism (Mitchell, 1979). Even in the absence of significant direct use of energy, the modern consensus is that they "earn their keep" indirectly through comminution and relationships with soil microflora. In reviewing standardized results of exclusion experiments, Seastedt (1984) calculated an average contribution by microarthropods of 23% to reduction of standing litter crop. Much research has gone into explaining results from these "black box" experiments, reviewed most recently by Seastedt (1984).

Saprophagous and mycophagous mites, particularly oribatids, influence soil structure by comminution of organic inputs, the production of fecal pellets and perhaps the prevention of fungal matting. Burrowing activity is limited to internal tissues of leaves, petioles, twigs, etc. and mineral particles are rarely ingested, or at least rarely reported (Harding and Stuttard, 1974). The only clear instance of organic-inorganic soil mixing by a mite seems to be that reported by Robaux *et al.* (1977), who, under laboratory conditions, found that *Tyrophagous*

putrescentiae can create mixed microaggregates in clay soil and increase aeration by the formation of cavities. Direct vertical and lateral translocations of organic matter are probably insignificant, since soil mites are rather sedentary on a diurnal basis and generally defecate on or near their food source. The significance of fecal pellet production by soil mites and collembolans is usually considered to be the increased surface area (relative to uncomminuted material), increased water-absorbing qualities, higher nitrogen concentration, higher pH and their small size, which allows illuviation into lower soil horizons. All these actions purportedly increase microbial activity, especially that of bacteria, as bacterial populations flourish in the higher pH regimes of the gut, feces and lower horizons. Since bacterial activity is a surface phenomenon, constantly requiring fresh surfaces (Luxton, 1981e) the comminution aspect seems especially important. When feeding occurs on leaf mesophyll, for example, not only is new surface exposed, but the food particle itself is subjected to decomposition in the gut and in the fecal pellet eventually formed. Increases in surface area due to fecal pellet formation are modest, however. Nef (fide Harding and Stuttard, 1974) found a 10,000-fold increase in surface area of a conifer needle when comminuted by a phthiracarid mite, but reformation into pellets reduced this to a 4-fold increase.

Although fecal pellets may decompose readily in certain situations (e.g., Jongerius, 1963), especially when moved downward in the profile, they are often rather long-lived (Grosbard, 1969; Webb, 1977; Bal, 1982) and accumulate, especially in mor soils with few large invertebrates to actively mix materials. Webb (1977) has noted that high cohesive forces between pellet particles, especially very small ones, are apparently the cause of this general recalcitrance, which is not observed with feces of larger arthropods. The most important function of small fecal pellets may be that they maintain the highest possible surface area for decomposition. He suggested there is a theoretical lower limit to size of free particles in the soil, and if not compacted into pellets the bite-sized particles would form even larger aggregates. Other work suggests that the increased surface area of mite fecal pellets is ineffective in increasing decomposition of the contained material. For example, the decaying grasses studied by Grosbard (1969) showed rapid decomposition after being fed upon by mites, but the fecal pellets decomposed very slowly. Perhaps mite feeding has an ecological cost associated with it, especially in the absence of soil mixing, or the slower decomposition of feces may serve an important regulatory function in some situations. The overall impact of comminution by saprophagous mites on soil structure and decomposition depends to some extent on the proportion of annual organic input which they ingest. Recent studies (Mitchell, 1979; Thomas, 1979; Luxton, 1981e) suggest that the figure may be almost insignificant (less than 2%) although few soil types have been studied. However, a small amount of feeding may go a long ways toward opening up new substrates for microbial decomposition. Equating mite ingestion rates with their contribution to decomposition processes maybe as fallacious as equating the metabolic contributions of soil animals to their importance in soil systems.

For two decades the concensus has been that the real importance of saprophagous and mycophagous mites and other microarthropods has been in their interactions with the soil microflora (the "catalytic" effect of Macfadyen, 1961). Most recently these interactions have been viewed in relation to nutrient element cycling. While microarthropod bodies have been implicated as potentially important sinks and sources of nutrients (Crossley, 1977; Luxton, 1979; Wallwork, 1983), their low standing crops make the amount insignificant in relation to quantities immobilized by microorganisms, particularly fungi (Seastedt, 1984). The principal significance of mycophagous mites seems to lie in their ability to extract limiting nutrients (e.g.,

nitrogen) from fungal standing crop and, with their death or excrement, make them available for rapid reuse in further mycelial or bacterial growth, with concomitant organic substrate decomposition (Whitford and Santos, 1980; Seastedt, 1984). As with comminution, the impact of soil mites will be some function of the amount of fungal tissue consumed. Estimates are rare, but consumption may be quite low in relation to fungal standing crop (Mitchell and Parkinson, 1976). The relationship of soil mites and other microarthropods to nutrient dynamics is complex (Seastedt, 1984) and whether their feeding helps fungal growth, or suppresses it and shunts decomposition to bacterial pathways (which may be more rapid and complete), depends on characteristics of the site, the substrate, and the organisms involved.

Considering their high densities, taxonomic diversity, conservative population dynamics, and a broad mix of specialized and opportunistic feeding habits, oribatid mites seem to be stable background decomposers, analogous in a way to most predaceous arachnids in that they seem incapable of rapidly adjusting to changes in resource availability. Crossley (1977) has contrasted this K-strategy to the r-strategy of collembolans, which may dominate microbial feeding at times of rapid growth; the r-strategy may also characterize fungivorous Prostigmata.

To better understand these processes we need more detailed information on feeding specificities of caprophagous and mycophagous mites, not just what will be eaten, but the physical and chemical cues which provoke feeding (Cancela de Fonseca and Poinso-Balaguer, 1983). We also need comparative information, from a wide variety of habitats, on the portion of organic matter input comminuted by oribatid mites and similar estimates on consumption of microbial standing crops by mycophagous mites. Comparative studies of longevity of fecal pellets and the extent and role of their bacterial enhancement in subsequent decomposition will also be important.

Some Additional Areas Needing Attention

Many other aspects of the biology and ecology of saprophagous and mycophagous soil mites are in need of continued study, and these can be used to illustrate or test many current general hypotheses. Biotic and abiotic determinants of community structure and microdistribution are known only in very general terms (see Anderson, 1975; Usher *et al.*, 1982; Wallwork, 1983). The importance of competition in determining coexistence of similar saprophagous and mycophagous mites (*e.g.*, Anderson, 1978) is an especially timely subject. Are the consistent size differences observed between coexisting pairs or series of congeneric oribatid mites (Walter and Norton, in press) due to limiting similarities imposed by exploitation competition (if so, what is the resource?), or are they simply manifestations of reproductive isolation mechanisms? Much remains to be learned about the distribution and biology of deep-soil mites, especially the Prostigmata (Kethley, in press). Gerson (1983) has recently suggested that filtrates from surface organic substrates may be an important resource for such animals.

Inter- and intra-habitat dispersal is another aspect which is virtually unstudied. We have some knowledge of dispersal in species restricted to specialized, insular microhabitats (*e.g.*, Binns, 1982; Norton, 1980), but knowledge of the potential for colonization (and redistribution within habitats), is important, especially in studies of perturbation effects. The use of soil arthropods as indicators of soil conditions and disturbances is in its infancy (Lebrun, 1979) but suffers from the paradox that many responses are species-specific, yet the diversity and inadequate state of taxonomy for most groups (see below) makes identification extremely difficult, even for "experts." The list of necessary research in biology is long, and the challenges are many, even without entering more basic areas of physiology, functional morphology and

genetics.

SYSTEMATICS

As has been echoed many times by ecologists and systematists alike, sound systematics is prerequisite to sound biology and ecology (e.g., Wilson, 1971). This does not simply mean having good species descriptions and monographs available. Well-corroborated hypotheses on patterns of evolution (phylogenies) are essential in attempting to put biological attributes and problems in an evolutionary perspective. That this "echo" has most often fallen on deaf ears can be easily seen in the fact that despite the ubiquity and diversity of saprophagous and mycophagous soil mites, in all of North America a single research position is devoted to study of their systematics (Dr. V. Behan-Pelletier, B.R.I., Ottawa).

As with the biological section, I deal here primarily with those soil arachnids of most interest with regard to soil structure and fertility, and make no attempt to summarize knowledge of major predaceous groups. Edaphic members of Mesostigmata represent about 120 genera in 30 families (Krantz and Ainscough, in press). Currently no North American monographic works, comparable to the European works of Karg (1971) or Ghilyarov and Bregetova (1977), are available. However, a valuable contribution has been made recently by Krantz and Ainscough (in press), who provides generic keys and references. Dondale (in press), Edgar (in press) and Muchmore (in press) have provided keys and guides to the literature for soil spiders, harvestmen, and pseudoscorpions, respectively. Of particular importance is the fact that the long-neglected erigonine linyphiid spiders (Micryphantidae) which are abundant and diverse in soil litter, are currently receiving attention (e.g., Millidge, 1983).

Saprophagous and Mycophagous Soil Mites: Descriptive Taxonomy and Monographs

Kethley (in press) has provided a family key and comprehensive reference list for soil Prostigmata, but no North American monographs comparable to those for the Palearctic fauna (e.g., Schweizer and Bader, 1963; Ghilyarov, 1978) currently exist, although a few families are known in some detail, at least at the generic level. Many species-level determinations even in common mycophagous groups such as Eupodidae, Pygmephoridae, Scutacaridae, Tarsonemidae, and Tydeidae are impossible. Of the approximately 14,000 described species of Prostigmata in the world, Kethley (in press, and 1982) suggested that nearly 6,400 (678 genera in 57 families) are associated in some way with the soil/litter community, and that less than 100 are mycophages. For those familiar with the true diversity of the aforementioned families in soils, it is obvious we have a long, long way to go in descriptive taxonomy.

Oribatid mites are perhaps the most successful of all soil arthropods (Johnston, 1982). The approximately 6,500 known species-group taxa represent more than 1,000 genera in about 150 families. As in most other mite suborders, the known species constitute a small fraction of the extant number. For this group also, there are no monographs for the North American fauna, or any substantial part of it. In contrast, monographic works on the Palearctic fauna steadily appear (e.g., Sellnick, 1928, 1960; Willmann, 1931; Bulanova-Zachvatkina, 1967; Kunst, 1971; Ghilyarov and Krivolutsky, 1975; Suzuki, 1978; Niedbala, 1980; Balogh and Mahunka, 1983). Whereas careful use of these works can be helpful in identifying the nearctic oribatid mite fauna, special care must be used in assigning species names. The North American literature is replete with wrongly applied names of European species. Especially helpful have been the several generic-level world or holarctic monographs of Balogh (e.g., 1965, 1972), but the

inadequate state of knowledge of the Nearctic fauna makes the distributional information in these works misleading. Also, generic concepts in many families, developed primarily in Europe, are not applicable to the North American fauna.

Ever since their serious initiation at the turn of the last century, in the works of Nathan Banks, descriptive studies on North American oribatid mites have been the domain of only one or two productive researchers, and the quality of work has varied tremendously. All of this will be referenced in a catalogue of oribatid mites of Canada and the continental U.S., which is nearing completion by Drs. V.G. Marshall, R.M. Reeves and me. It lists approximately 1,000 species-group taxa and will be especially important as a guide to the literature. It does not substitute for much-needed monographs, however, and as in other soil mite groups, the taxonomy of North American oribatid mites is not yet "user-friendly."

One problem with most mite monographs is that they do not deal with immatures. Whereas in most Mesostigmata and many Prostigmata the immatures and adults are easy to associate, this is not so for the brachypylinae, or "higher" oribatid mites, which are the most abundant and diverse groups in most soil extracts. If extractions are efficient, immatures are obtained in high numbers and much information is lost by lumping them as "oribatid nymphs." The only key available for immatures is that of Wallwork (1969), and this is necessarily very general and incomplete. Although the importance of immatures in systematics and ecology has been stressed (*e.g.*, Grandjean, 1953; Trave, 1964) relatively few researchers make the effort to describe them.

Supraspecific Classification and Phylogeny

Before concluding, a few statements should be made about trends in the classification of soil arachnids, and the general philosophical issues behind them. Historically, most classifications have been based on *differences* between groups of organisms and little distinction was made between classification and identification, which should be quite opposite procedures. Classifications have tended to be pragmatic mirrors of identification keys, but the price paid for such a simple translation is loss of the evolutionary perspective. Like keys, classifications based on differences, tell us nothing about evolutionary relationships, which can only be deduced from patterns of *similarities* between groups. As an example, let us examine the recent classification of enarthronote oribatid mites by Balogh and Mahunka (1983) (their Arthronota). Two cohorts are recognized within this group, the Euarthronota and Arthroptyctima. The first has nine superfamilies, all with a single family. The families are so separated because of discrete morphological differences. The Arthroptyctima has two superfamilies, each with a single family. While this classification could readily be translated into a key, it carries essentially no evolutionary information. The Arthroptyctima is biphyletic; the character on which the grouping is based (ptychoidy) is clearly derived by convergence so that the closest relatives of each of the two superfamilies are not each other, but are in different superfamilies of Euarthronota (see Norton *et al.*, 1983; Norton, 1984). Also, even though there is much to be learned about relationships in the families constituting Balogh and Mahunka's Euarthronota, some relationships are easily defined (Norton *et al.*, 1983; Norton, 1984) yet completely masked by their excessively split, redundant classification. Scientists who are seeking an evolutionary understanding of biological processes, such as the distribution of feeding strategies and their effects on soil structure and fertility, or adaptations to desert conditions, or whatever, are thus done a disservice.

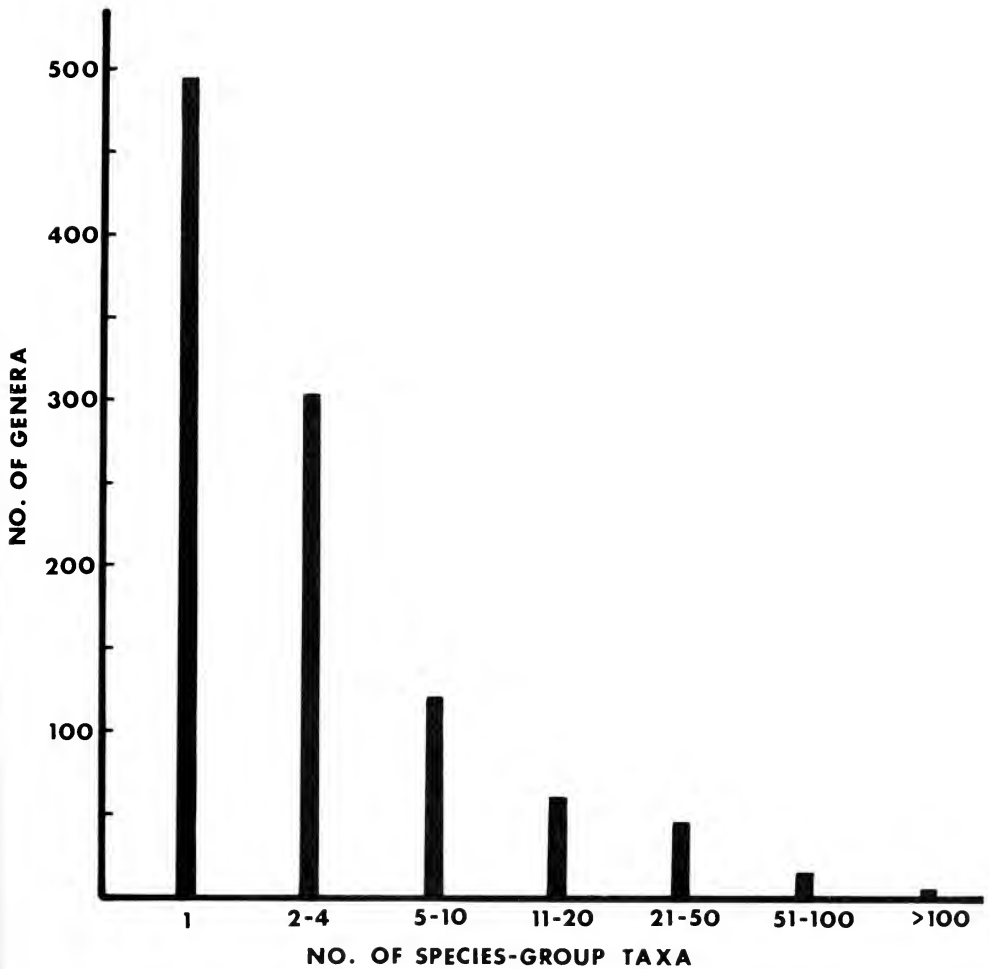


Fig. 1. Present distribution of species-group taxa among genera of oribatid mites (worldwide).

The effects of emphasizing differences can also be seen in the distribution of species and subspecies among genera (Fig. 1). Almost half (47%) of the approximately 1,000 proposed oribatid mite genera are monotypic and three-quarters have fewer than five species-group taxa. The trend is also growing; in 1980, the monotypic genera constituted 43% of the total. Clearly the reason is an emphasis on differences for purposes of identification and results in the same loss of evolutionary information.

Classifications based on similarities, in particular similarities which are evolutionary "novelties," are becoming more popular. Such classifications require more thought and effort. They are based on the development of testable hypotheses of evolutionary patterns, or phylogenies, the techniques for which are grouped under the rubric "cladistics" or "phylogenetic systematics" (see Wiley, 1981). It is not always possible or even necessary to develop phylogenies when doing descriptive work, but the principle of "classification by

similarity" can be adhered to, nonetheless.

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BIOLOGICAL AND SYSTEMATIC PROBLEMS INVOLVING SOIL DWELLING ARTHROPODS

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ABSTRACT

Study of structure, classification, and way of life of myriapods is still in a threshold position, and ground is being lost rapidly because current researchers are not only numerically fewer than in the past, but are less productive. Ironically, at the same time, their research potential is becoming appreciated, and a rapidly increasing interest in these animals is being shown by ecologists and other biologists. Regrettably, a number of important major discoveries in myriapod biology during the past 30 years have been left fallow, after their discoverers died or turned to other subjects. The present deficiency in alpha and beta taxonomy has had a negative effect on other areas of research: it is not very useful to investigate organisms which are nameless and unclassified. The obvious solution to the problem is to increase the number of systematists and provide the necessary outlets for major revisionary studies. If necessary, funds should be diverted from well-known but still intensively studied groups like terrestrial vertebrates and angiosperms, and allocated to inadequately known and even less-studied organisms of the soil, on which all terrestrial life ultimately depends.

RÉSUMÉ

Certes on a souvent dit que la taxonomie, la morphologie et l'histoire naturelle des Myriapodes sont encore dans leur enfance, et que ces domaines prennent même actuellement du recul parce que les chercheurs y sont moins nombreux et moins productifs que par le passé. Ironiquement par contre, les écologistes et autres biologistes montrent un intérêt croissant pour ces animaux, dont ils réalisent le potentiel en matière de recherche. Il est fort regrettable que plusieurs percées importantes dans l'histoire naturelle des Myriapodes ayant eu lieu au cours de 30 dernières années n'aient point connues de suite après que leurs découvreurs soient décédés ou aient changé de champ d'étude.

La déficience actuelle en taxonomie alpha et bêta a évidemment un impact négatif sur les autres domaines de recherche: il n'est pas très utile d'étudier des organismes qui ne sont ni nommés ni classifiés. La solution évidente à ce problème est d'augmenter le nombre de systématiciens étudiant les Myriapodes et d'offrir les débouchés nécessaires pour d'importants travaux de révision taxonomique. Si cela s'avère nécessaire, des argents supportant présentement des travaux sur des groupes bien connus mais malgré cela encore sur-étudés, tels que les Vertébrés et les Angiospermes, devraient être redistribués pour soutenir des projets d'étude de groupes mal connus et encore négligés d'organismes du sol, desquels dépend ultimement le maintien continu de toute vie terrestre.

INTRODUCTION

It is common for scientists in virtually any discipline, no matter how sophisticated it may have become, to deplore deficiency of knowledge in their specialty. I suspect, however, that the participants in this symposium are, by virtue of their own experience, disposed to accept a general *apologia* that existing knowledge about myriapods is strikingly deficient and fragmentary. It is certainly not an overstatement to note that myriapodology – and such a word

is not even in dictionaries – is presently at the same level of development as was entomology about 1850, or ornithology about 1800.

Many persons whose knowledge of Myriapoda derives from standard texts published in the recent past, consider this group to include few orders of insignificant classes, and are surprised to learn that diplopods alone constitute 15 orders and about 115 families. There is more to the subject than *Julus*, *Spirobolus*, and *Lithobius*, and the major problem that I had to face on being invited to summarize current “state of the art” for the four myriapod classes was how to do it meaningfully in 30 minutes. I have little confidence that such a goal can be achieved, even with rather superficial coverage. Three areas will be considered: present state of knowledge of myriapods; problems impeding an improved knowledge of them; and what is presently known about the impact of myriapods on the formation and characteristics of soil. Even for inadequately known taxa, this is a large order.

PRESENT STATE OF KNOWLEDGE OF MYRIAPODS

Systematics

To begin with, even the phylogenetic relationships of the classes Diplopoda, Chilopoda, Pauropoda, and Symphyla to each other and to the hexapod tracheates are far from being established. Much has been written on this point since about 1887, when R.I. Pocock established the first “modern” arrangement, aligning Diplopoda, Pauropoda, and Symphyla in a group Progoneata, and the Symphyla and Insecta in the coordinate Opisthogoneata. The most extensive recent work, and by far the most authoritative, has been that of S.M. Manton whose approach to the postulation of phylogeny was based largely upon comparisons of structural and functional aspects of locomotory systems. Without wishing to denigrate in any way the superb research conducted and published by Manton (1954–1977) with exceptional illustrations, I feel that her conclusions were seriously flawed by reliance upon an outdated classification (that of Attems, 1926, which was actually written near 1920), and by insufficient consideration of adaptive convergences. In particular, I cannot accept the notion that “myriapods” comprise a monophyletic entity coordinate to a comparable “hexapod” group as separated solely by a difference in mode of mandibular articulation. Single character differences between taxa do not inspire much confidence when they oppose groupings made on the basis of extensive similarities in numerous character-systems. I prefer to recognize an indivisible spectrum of tracheate classes, which awards class rank for collembolans, proturans, diplurans, thysanurans, and pterygotes, and which admits the numerous shared characters of diplurans and symphyliids. I am not aware at the present of any convincing arrangement of these five hexapod and four myriapod classes into higher groups (e.g., superclasses or subphyla). Depending on which character systems are stressed, any number of classifications could be devised, including one that sets Diplopoda apart in a sister-group relationship to the other eight combined. The fossil record has, so far, shed very little light on this problem.

Initially, “myriapods” were studied by general zoologists, then – up to about 1900 – by entomologists. The primary taxonomic characters of both pauropods and symphyliids are chiefly those of chaetotaxy and subtle modifications of the integument, and except for the advantage of improved optical equipment, the techniques involved in their study have changed but little in the past century. Similarly, the study of lithobiomorph and scolopendromorph chilopods still follows classical procedures of the last century (enumeration of spines, spurs, and sutures). But a fundamental change occurred in classification of geophilomorph centipedes around 1870, with Meinert’s discovery that the best familial and generic characters reside in mouthpart

structure. This realization instantly rendered all previous work on these animals obsolete, and mandated the eventual restudy of early geophilid types. A similar revolution in milliped classification was triggered in 1884, when Robert Latzel made extensive and effective use of male genitalia to distinguish both genera and species in the central European fauna. Genitalia had been sporadically described, and even illustrated, since 1832, but Latzel's consistent and comprehensive emphasis of these appendages was catalytic. Virtually all millipeds named prior to Latzel's time require redescription with respect to genitalic structure.

As the result of these important discoveries by Meinert and Latzel, generation of myriapod specialists emerged around 1890, some of its members being converted entomologists, some innocent of any previous tradition. A cadre of six dynamic young men working chiefly in the 1890s built the foundations of our existing classifications of the various myriapod groups, except for the Pauropoda and Symphyla. Working most of the time in isolation, some of them adopting inappropriate attitudes about taxonomy and nomenclature, they also provided a heritage of confusion, duplication, and outright systematic anarchy that by 1950 had attained epic proportions. Most of these pioneers endeavored to study the world fauna of both chilopods and diplopods (often the other two classes as well), and if their work was adequate in one class, it was usually catastrophic in the other. Recitation of the problems generated during this period would fill a volume, and a large part of modern work consists of tedious corrective surgery.

During this period, about 60 years in duration, of intense descriptive work, emphasis was placed on alpha taxonomy of the crudest sort, usually the naming of material in regional collections. Some of the most productive workers seemed to operate on the principle that the mere naming of taxa, without a word of comment, was the pinnacle of taxonomic achievement. It was not until the global catastrophe of World War II that this period came to an end, coincidentally with the demise of most of its major figures.

To illustrate the rather spectacular growth during this period I can provide two illustrations from the Diplopoda, the group I know best. The first is a table of higher taxa recognized at various time intervals from 1847 to the present. The figures are not absolute, as they do not take into account existing taxon names regarded as synonyms by the various authors cited.

Another way to show the same trend is with a line graph (Fig. 1) showing the increase in number of generic names cumulatively, without prejudice as to their actual status.

The almost explosive increase, beginning in the 1890s, is not much different from that in other major taxa, but begins much later than most, and represents the astonishing productivity of three persons: Carl Attems, K.W. Verhoeff, (1926–1932), and R.V. Chamberlin, who among them proposed no fewer than 1199 genera. One notices that the curve begins to level off after 1950, but this is purely a result of changing times and not a depletion of undescribed genera. Actually, two things have conspired to dampen the growth rate. First is a post-war change in taxonomic philosophy, from sheer mindless description of novelties as an end in itself to a strong emphasis on clean-up work: restudy of old types, preparation of whatever revisions could be managed, and so on. Second, and perhaps more compelling, has been the incredible increase in the costs of publication. (In these days of near-universal page-charges, it is refreshing to recall that Verhoeff, for instance, was actually paid – so many words per mark – by the *Zoologischer Anzeiger* and other German journals. Today only a millionaire could afford to publish the typical Verhoeffian output of several hundred pages per year.)

I believe that we have so far described about 20% of the actual milliped fauna of the world. If this figure be true also for the other three classes, a sum total of more than 100,000 myriapod species must be reckoned with.

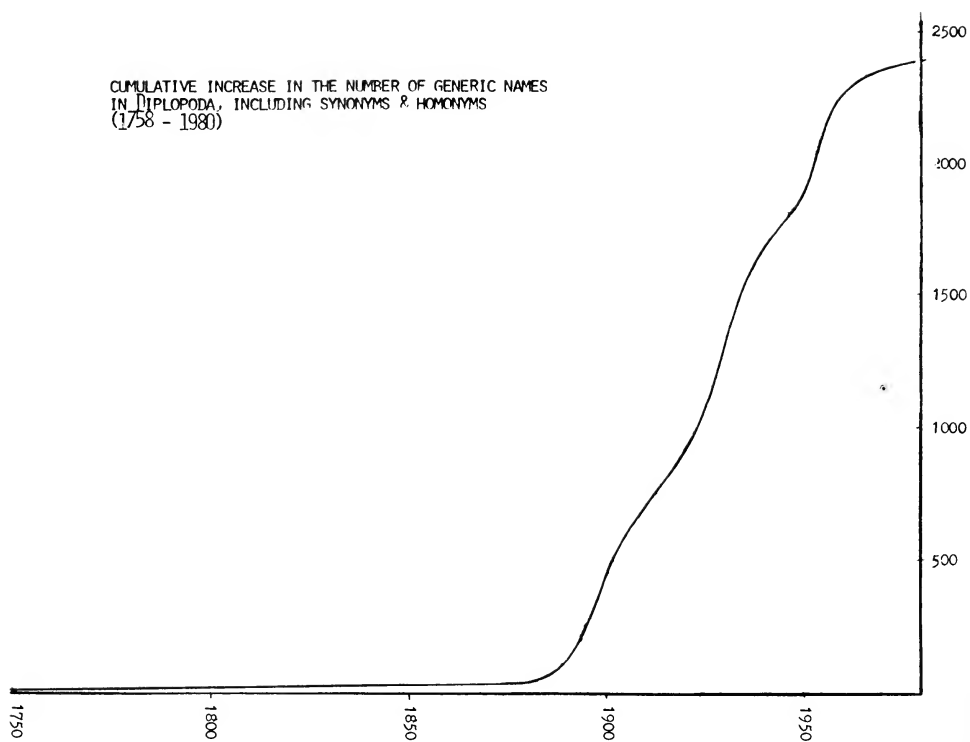


Fig. 1. Cumulative increase in the number of generic names in Diplopoda, including synonyms & homonyms (1758-1980).

Table I
Increase in the number of higher taxa, Class Diplopoda

Reference	Orders	Families	Genera
Gervais, 1847	1	5	16
Bollman, 1893	4	7	60
Cook, 1895	6	50	190
Silvestri, 1897	6	66	353
Attems, 1926	7	70	621
Hoffman, 1980	15	115	1701

The only comprehensive treatment of the classification, structure, and way of life of all four classes is that of Carl Attems, in the Kükenthal-Krumbach *Handbuch der Zoologie* (1926), which was written more than 60 years ago. The taxonomic part is of course hopelessly out of date, and was seriously flawed even at the time it was written, but for many taxa it still remains the only existing reference.

For Diplopoda, two recently published manuals are useful. One is a catalog of all generic and familial group names, with their type species, published from 1758 to 1957 (Jeekel, 1971). The other is a classification of the world fauna down to the level of subgenera, compiled by me (Hoffman, 1980). It contains no keys nor descriptions, but does include reference to all post-1926 synoptic taxonomic papers.

The enormous order Polydesmida was surveyed by Attems in three big volumes of the *Tierreich* series (1937–1940), but these works are chiefly useful from a bibliographic sense, being mostly compilations severely handicapped by their author's ultraconservative taxonomic philosophy. At least all polydesmoids described up to that time are included somewhere, and Attems' real contribution was to provide a beachhead for further, more refined studies. In recent years, some work, reminiscent of the labors of Hercules, has been conducted by a few hobbyists. The Paradoxosomatidae, largest family of the entire class, has been under study by C.A.W. Jeekel since about 1950. This author published a provisional classification of the group in 1968, as well as numerous generic synopses and clarifications of nomenclature, but his intended goal – a new revision of the entire family – is still a long way in the future. Since about 1955, I have been working in a similar way on the larger chelodesmoid families, e.g., the Chelodesmidae, Oxydesmidae, and Gomphodesmidae. Although revisions of many genera and tribes have been published, only the African family Oxydesmidae is now actually at the stage of preparation for publication. The Chelodesmidae will doubtless prove to be the largest family of Diplopoda: already more than 20 tribes and 200 genera have been defined even though the fauna of Brasil has scarcely yet been sampled. The family Xystodesmidae, virtually endemic to North America, is being worked up one genus at a time, beginning with the rich Appalachian fauna, by R.M. Shelley (e.g., *Sigmoria*, 1981). But the numerous families of "smaller polydesmoids" have received essentially no attention and at present nobody has either the time or interest to study them despite their importance in soil samples from any tropical region.

In the order Chordeumatida, characterized by a large number of mostly small disjunct families, some progress has been made chiefly on the Nearctic fauna by W.A. Shear, who has revised the Conotylidae (1971), the Cleidogonidae (1972), Rhiscosomididae (1973), and Tingupidae (1982). Dr. Shear advises me, however, that in less than a decade so much new material has accumulated as to render his cleidogonid monograph obsolete. Other students of this order, notably S.I. Golovatch and J.-P. Mauries, have published descriptive papers on the Old World fauna but do not appear to be contemplating comprehensive revisions. The study of this order is greatly impeded by the scarcity of material; a great many species still remain known only from the type series named decades ago.

The large, mostly tropical species of the order Spirostreptida have been recently, and adequately, summarized: the Spirostreptidae itself by Krabbe (1982), the Harpagophoridae (in part) by Demange (1961 *et seq.*), and the Odontopygidae by Kraus (1960, 1966). These large and useful papers go far to setting in order the classification of the three families, but still represent only a first step, and none of the many genera involved have yet been the subject of a "modern" revision. The cambaloid members of this order remain in a state of substantial confusion, with little agreement even about the definition of families, but the group is being

studied by Mauries and it is hoped that a revisionary monograph may be forthcoming in a few years.

Species of the related order Julida remain in a sort of limbo. The family Parajulidae, which is virtually endemic to North America, was studied for many years by N.B. Causey, but despite appreciable research nothing useful was published before Dr. Causey's death in 1979, and no one has touched the group since. A more optimistic statement can be made about other juloid families, which are now being investigated by Henrik Enghoff. It is the intention of Dr. Enghoff to eventually reorganize the classification of the entire order, and toward this end a number of preliminary studies have already been published.

Lastly, in the order Spirobolida, the family Spirobolidae was monographed in a very adequate way by W.T. Keeton in 1960. This group is in a good condition for detailed biosystematic studies of individual genera. The other spiroboloid families – such as have been adequately defined – remain in complete chaos, and identifications of rhinocricids, pachybolids, and trigoniulids are virtually impossible to make.

Many families, especially in the Palearctic region, are monobasic or nearly so, and their revision would entail only careful studies of structural features and comparisons with related taxa. Omitting such groups, and in summary, less than 10 families of Diplopoda have been recently treated taxonomically in a way useful to beginners, *e.g.*, with keys, diagnoses, illustrations, synonymical lists of species, maps, and other features normally taken for granted by students of most other animal groups.

From a faunistic standpoint, the record is not much better. Checklists are available for North America (Chamberlin & Hoffman, 1958) and Mesoamerica (Loomis, 1968); both are not considerably outdated. National surveys are available for Great Britain (Blower, 1955, and in press), Germany (Schubart, 1934), France (Demange, 1981), India (Attems, 1936), and Japan (Miyosi, 1959). One of the best-known parts of the world for diplopods is the Union of South Africa, thanks to the work of Attems (1928, 1934), Schubart (1956, 1958, 1966), and Lawrence (numerous papers, *e.g.*, 1953a and b, 1967). A few unlikely parts of the world have been treated faunistically, such as the island of Hispaniola (Loomis, 1936) and Panamá (Loomis, 1964).

Centipeds are probably even more inadequately-known than millipeds. A catalog of generic names and their type species has been compiled by C.A.W. Jeekel but not yet published, and there is no classification of the Chilopoda *in toto* since 1926. The order Geophilomorpha was treated in the *Tierreich* series by Attems (1929) and the Scolopendromorpha by the same author a year later (1930). Aside from being decades out of date, both of these manuals were largely compiled from faulty literature and were inadequate the day they were published. The content of both orders has virtually doubled in the past fifty years, with no reliable update. The enormous and difficult order Lithobiomorpha has not been treated comprehensively, nor has the much smaller Scutigleromorpha.

Regional papers have been published for Great Britain (Eason, 1964), France (Brolemann, 1935, Demange, 1981), and South Africa (Attems, 1928). The Lithobiomorpha of the Soviet Union was treated by Zaleskaja (1978) and the North American species of this order were covered in an excellent series by R.V. Chamberlin (1913–1925). Unfortunately, the good start embodied in the last-cited reference was promptly subverted by a long sequence of unsatisfactory “descriptive” papers by the same author during the following 30 years. The often cryptic synonymy and nomenclature of lithobiids has been clarified over a period of time by E.H. Eason, who hopes to prepare a world catalog for this large and difficult family. A good

start was made toward reclassification of Geophilomorpha by R.E. Crabill during the years 1960–1968, but regrettably no major synthesis was published before his retirement in 1983. Recent, outstanding work on this order is being published by L.A. Pereira, who expects to revise initially the family Schendylidae, and eventually other geophiloid taxa as well. The chilopod fauna of southern Europe, particularly Italy, is being studied by A. Minelli.

No optimistic statement can be made about the classes Pauropoda and Symphyla. At present, both of them are virtually the exclusive domain of Ulf Scheller. The scarcity of good material in both groups, and the very fragmentary geographic representation, renders revisionary studies almost impossible. Scheller's faunistic studies, however, are models of excellent presentation and include as much group taxonomy as can be managed. So many pauropods are cosmopolitan or nearly so, that a world synopsis of this class is necessary for adequate work, and at present this can be gained only by knowledge of the entire published taxonomic literature in the original. It is possible that Dr. Scheller will prepare a catalog of the species of one or both classes.

Concluding this somewhat discouraging summary of myriapod classification at the present time, a glance at the number of current active specialists cannot fail to give an even gloomier prospect for the future:

Chilopoda: England, 2; France, 2; Italy, 1; Australia, 1; Argentina, 1; U.S.S.R., 2; total: 9.

Diplopoda: U.S.A., 3; France, 2; Denmark, 1; Germany, 1; U.S.S.R., 2; Japan, 2; Holland, 1; total: 11, two of which are duplicated in the chilopod list.

Pauropoda: Sweden, 1; Austria, 1; Germany, 1.

Symphyla: Sweden, 1.

Most of the foregoing specialists are either teachers or curators; in either case, their research time is limited (or outright stolen from primary obligations). Nearly half of them are nearing the end of their productive years. All are inundated with material, and years behind on projects and gratuitous identification work. At most, only about five persons are relative newcomers to myriapod taxonomy.

Morphology

What can be said of taxonomy's sister science, morphology? Outstanding anatomical studies have been made in recent years by Demange and by Manton. The latter author dealt primarily with integumental and musculature modification associated with locomotion. Demange published an outstanding study on thoracic segmental musculature in 1967, with many profound implications (some of them controversial). I do not know any subsequent researches extending, confirming, or refuting the findings of these two pioneers. It cannot be said that the study of even the general aspects of structure of myriapods has been exhausted, and I cite a few examples. (1). A good comparative study of the head capsule amongst diplopods has not been published, nor has an attempt been made to homologize head musculature with that of body segments. (2). Species in several spiroboloid families have paired paramedian dorsal pits on each segment, of totally unknown function. (3). In the family Paradoxosomatidae, many species have glands opening through paired pores on the 5th sternum: such glands have not been mentioned by anybody and I suppose have been overlooked to the present. Obviously their function likewise remains unknown!

For Chilopoda, at least, the areas of ignorance have been categorized in Dr. John Lewis's recent (1981) book on centiped biology; someone seeking structural, developmental, or ecological problems can find one on nearly every page. Some come at once to mind. (1). Many

geophiloids have conspicuous sclerotized sternal pits, much used in taxonomy but of totally unknown function. (2). What is the function of the Tömösvary Organ? (3). What is the function of coxal pores in lithobiomorphs?

Only within the past two decades has anything been done of note with the neurosecretory structure of centipeds (or millipeds, for that matter). The same time period has seen the initiation of work on microstructure of muscles, of sperm cells, of sensory organs. As many as a dozen papers have been published in these areas. But since something has to be skimmed over in this review, the cut is in structure: there is much to cover yet.

Embryonic development of millipeds was first studied in the last century by Metschnikoff, Newport, and Heathcote. Several papers were published by Silvestri (*e.g.*, 1950), Pflugfelder (1932), and most recently and thoroughly, by Dohle (1974). Details of development for many orders remain unknown, including those for the exceptional group Stemmiulida in which the young eclose with 19 segments instead of the six common to all other diplopods. Demange has observed that embryos of most groups reveal little information about phylogeny because many critical structures do not appear in the early stages. Yet, there is plenty of opportunity for a student to make a distinguished career in this area.

Much happens after hatching. In many milliped groups, the male genitalia begin to modify from normal walking legs early in the stadium sequence, becoming larger and more specialized with each moult. In polydesmoids, however, the final moult changes a small knob-like primordium into a mature gonopod of often fantastic complexity. Nobody has sectioned specimens during this diapause period to follow the sequences of events, to determine what pattern may exist comparable to the mechanisms that direct the reorganization of holometabolous insects during pupation. Development of the modified posteriormost legs of male lithobiomorph centipeds has not been studied, either.

Way of Life

The foundations of present knowledge about myripod way of life were laid down chiefly by K.W. Verhoeff, who studied the Palearctic fauna for half a century. Verhoeff (1926–1932) worked out the life histories of many kinds of millipeds and centipeds, and discovered the interesting phenomenon that occurs in various kinds of julids: non-mating intercalary adult males ("Schaltstadium") which moult into a sexually active stage. This subject has been carefully studied in England by J.G. Blower and some of his students, and in France by F. Sahli (*e.g.*, 1969). In general, postembryonic development, particularly of julids, occurs in a number of remarkable patterns, in many taxa with stadia omitted or added. Blower's group has also worked on population structure, phenology, and general natural history of various British millipeds, and provided a fine model for those who might wish to study the fauna of other regions (*e.g.*, Blower & Gabutt, 1964; Blower & Miller, 1974). Fundamental work on way of life of *Ommatoiulus moreleti*, an Iberian julid introduced into South Africa and Australia, is being conducted by G.H. Baker (1978a-c).

Details about life history have been published for only two North American millipeds (and no centipeds), and these are not comparable to the precisely executed studies of European investigators. A few papers have referred superficially to habitat preferences of American species, contrasting with the careful work of J.-J. Geoffroy (1981) on the French fauna. Interactions of myriapods with other organisms and with their environment have rarely been better-accounted than in R.F. Lawrence's notable book about South African soil fauna (1953).

Diplopods were considered to practice only the most perfunctory kinds of reproductive behavior. During the past two decades, publication by Ulrich Haacker (1969), in Germany, reported fairly sophisticated courtship practised by some julids, the males of which preferred an attractive secretion from the base of the 2nd pair of legs, which attracted (and distracted) females which fed upon the material whilst the male inobtrusively effected copulation and sperm transfer. Haacker (1971) also reported apparently similar glands located middorsally on the terga of several European chordeumatids, but was not able to observe their actual use. In other studies (1968) he taped and analyzed the stridulation of South African sphaerotheriids, produced by males as an element in courtship. Lamentably, this gifted investigator died at an early point in his career, and nobody has since continued along the trail he blazed so well. Regrettably, detailed studies of reproduction have not been reported for a single North American millipede. The considerable body of published field and laboratory observations has not been organized for second-stage, follow-up work. One facet that merits careful study is the sociality of platydesmid species, represented most conspicuously in the United States by the genus *Brachycybe*. These animals tend to live in large aggregations of all stages, and in such colonies specimens are often seen in a stellate arrangement, heads together, bodies radiating out like spokes, for a still-unknown reason. In this genus, large numbers of tiny yellow eggs are released by the females, then gathered up and brooded by males, an exceptionally rare occurrence among arthropods. The phenomenon was observed by me in North Carolina in the summer of 1958; by an astonishing coincidence it was published in the same year by Y. Murakami for a Japanese species of *Brachycybe*. Careful studies remain to be made for other platydesmid genera in North America and the Mediterranean region. Do they share this trait? How could such deviant behaviour have developed?

Males of many diplopod taxa, particularly polydesmoids, are provided with a complex arsenal of secondary sexual modifications of legs, sterna, and mouthparts. How such equipment is used remains completely unknown, and could be elucidated by just the simplest observation of mating pairs. Some is obviously involved in clasping the female, some, involving internal glands and their pores, must perform an attractant function. Mauries (1969) described the mating behaviour of *Typhloblaniulus lorifer*, in which coupling and positioning of the female is achieved by intertwining of the bodies, by the female biting the modified 1st legs of the male, and by the female's antennae being clasped by a modification of the male's mandibles. Species of the allied family Parajulidae occur in abundance over much of North America, adults exhibit a wider variety of sexual modifications, and yet not a single observation has been published on reproductive aspects of this big family. There is also a capital problem involving *Aenigmopus alatus*, Guatemalan polydesmoid males, which lack gonopods: how does it accomplish sperm transfer? This species is known so far only from type material, but a precise locality is known and it should be possible to obtain living specimens.

Prior to about 1957, virtually nothing was known about the mating behaviour of chilopods. Using infra-red light for observations, H. Klingel solved this riddle and reported his findings in several papers (e.g., 1957, 1960). Apparently little has been done since that time. It is well-known that the males of numerous American lithobiomorph genera have the last pair of legs modified in curious ways: a spectrum of knobs, crests, cavities, hair tufts, and pore fields. Could not some student of behaviour adopt Klingel's techniques to see what role these strange modifications play in mating? Do females recognize corresponding males tactily?

It has been known for years that millipeds produce a variety of caustic and/or aromatic secretions when disturbed, the odours being variously reported subjectively as like camphor,

almond extract, osmic acid, quinine, creosote, and rotting sponges. A few chemical analyses were made during the first half of this century, but scientific studies on allomones were really first initiated by Thomas Eisner about 25 years ago. Eisner investigated not only the chemical composition of these secretions but their biological functions as well. Aside from the obvious role of predator deterrents, most of the secretions are markedly fungicidal, suitable for organisms which live in damp biotopes (Eisner, 1970). The structure of the ozadenes was worked out by D.W. Alsop in Eisner's laboratory, but details have, to the best of my knowledge, not yet been published. Biosynthesis of benzaldehyde and hydrogen cyanide, common ingredients in polydesmoid allomones, was worked out by Duffey, Underhill & Towers (1974) in *Harpaphe haydeniana*, a common species in British Columbia. Substantial progress was made at the University of Georgia (cf. Duffey, 1977) toward possible chemotaxonomic use of allomones, but once again, a promising start soon faltered and nothing is currently being done along these lines. Existing evidence suggests a fairly close correlation between allomone structure and established taxonomic groups.

Some millipeds are known to be luminescent, a phenomenon especially well developed in some Californian xystodesmids, reported by Davenport (1952), but with inconclusive evidence about the cause. Some geophilomorph centipedes emit a phosphorescent secretion from sternal glands, but to what end remains unknown. Most geophilomorphs are some shade of yellow, brown or red. The small species of the tropical family Ballophilidae, however, depart from this norm in their colouration: bright blue, violet, purple, green, and black species are known. Ballophilids are characterized in part by having the sternal glands open onto a midventral sternal knob, and in fresh specimens the glands can be easily seen as clusters of intense pigmentation through the more dilute colouration of the integument. What is different about ballophilids and their sternal glands? No one has any idea. Not even the crudest histochemical assay has yet been attempted.

The foregoing enumeration of some areas of ignorance has largely avoided mention of either pauropods or symphylids. It is hardly necessary to add that virtually nothing is known about the structure and way of life of members of more than one or two common European species.

IMPEDIMENTS TO DEVELOPMENT OF MYRIAPODOLOGY

I am sure that those who study mites, nematodes, springtails, or pseudoscorpions will be surprised at little I have said so far: most soil organisms share this heritage of neglect. No doubt all of us tend to agree that problems such as the following are serious ones:

1. Virtual ignorance of the actual fauna in many parts of the world, especially the tropics, and frequently there is a burden of inadequate taxonomic and complex nomenclatorial problems afflicting even the better-known faunas.
2. The likelihood that major parts of the world's soil fauna will become extinct before it can even be sampled. Berleseate samples now in dead storage in various museums probably contain a number of already extinct species: fossils in alcohol.
3. Difficulty of entry into the classification and identification of most groups because the literature is extensive, fragmentary, widely scattered, and polyglot.
4. The frequent impossibility of obtaining identifications because either there are no specialists, or, if such exist, they are 35 years behind their unidentified backlog, or, worse, unable to make an identification without having first to revise the genus, tribe, or family involved.

I may be forgiven my bias in believing that organisms must be described and placed in a classification before information about them is meaningful. Taxonomy may be *passee* in ornithology and some other mature fields of zoology, but I am appalled to observe how many people are still investing vast resources of time and money deciding whether a given vertebrate taxon is a good species, a sibling species, a subspecies, or what, when the majority of arthropods are still unknown, uncollected, and ignored. Is it a better investment to investigate details in vertebrates, or get on with the higher classification of other phyla?

Solutions are fairly obvious. Most of the present generation of myriapodologists drifted into this area accidentally, and remained in active pursuit of research goals primarily as a personal hobby, with time abstracted from career requirements and family obligations. Even museum curating is no ideal occupation, if one is primarily responsible for the collections first, routine identifications second, and perhaps personal research last. If more taxonomists are needed to handle the job of working up what we have already in museum jars, some better way must be found to employ their talents on an occupational basis. What graduate student wishes to invest quite some years in learning the complexities of myriapod lore, if there is no hope whatever for finding gainful employment in such a specialty? Research on structure, behaviour, and ecology can be left to academic sectors. These are areas which can be rather quickly comprehended, pursued, and solved in segments by graduate students. Systematic work, in my view, requires a far longer time to master, and productivity is linked with continuity. I began the study of millipeds as an undergraduate, as did several of my friends, but could not do so today simply because I could not cope with publication problems. If progress is to be made in myriapod taxonomy not only must career opportunities be guaranteed, but possibilities for publication of taxonomic monographs must also be improved. Many of the better-known research-support sources (I may mention the U.S. National Science Foundation) award grants on an egalitarian basis: as much is given for studies of vertebrates (less than 1% of animal creation) as for arthropods (more than 90%). Is it possible to redistribute the available largesse on a scale commensurate with the actual size of the group, and its need for study? I strongly support the principle of peer evaluation of research proposals, but appeal for reason in the process. I have known excellent, deserving projects turned down because one or two reviewers felt that the applicant should have introduced reference to "phenetics" or "cladistics" or some other popular fad. In work on many groups of arthropods, we are still trying to scramble into the lower levels of *beta* taxonomy. We must crawl before we fly, and to impose a requirement for theoretical biology when there is no existing base for it, seems entirely unrealistic and counter-productive.

MYRIAPODS AND SOIL

Lastly, it is necessary to append a few remarks appropriate to the subject of this conference. I have investigated the historical background as far as the paper by Shaler, which first suggested a substantial role of diplopods in soil formation; also the classical texts written or edited by Kevan, Raw, and Schaller, also recent papers by van der Drift, Gere, and other European workers. Most publications so far relate to diplopods, and are in two categories: some subjective field observations lacking quantitative controls; and laboratory experiments not closely associated with natural conditions.

Two areas of actual soil influence are generally accepted: physical and chemical. The first involves disruption of the upper layers of soil and the litter accumulation by burrowing activities of diplopods. Many of these (which may be surface or even arboreal dwellers when

mature) may spend all of their immature stadia burrowed fairly deeply in the soil itself: the general collector rarely finds young millipeds in the upper horizons. Scolopendromorph and geophilomorph centipeds likewise burrow to some extent, or exploit the burrows of other animals. I think that either exclusively edaphic residence, or vertical circadian movement must be accounted a substantial influence on the physical makeup of upper soil strata, although I do not know of any work quantifying the effect. It is well-known, secondarily, that most millipeds are detritivores and break down a lot of vegetable material (leaves, rotting wood, fungi) simply by mechanical trituration as they feed upon it. Some earlier authors (Romell, 1935; Eaton, 1943) implicated millipeds as a major factor in mull formation, and certainly captives are able to reduce a handful of decomposing leaves in short order, as can be confirmed by anybody who keeps a live spirobolid under observation. But I am often amazed to sift through really large quantities of leaf litter in apparently optimal situations without finding a single milliped of any species, and humification proceeds apace. So far as I know, all chilopods are carnivores, and pauropods and symphylids probably poelomicrophaghes; these groups probably contribute very little to mechanical litter conversion.

Chemical influences are of several kinds: modification of plant material through digestion; uptake and concentration of calcium and other minerals; release of nitrogenous compounds from metabolic excretion; and formation of weak organic acids as the result of death and protein breakdown. Most of these factors have been alluded to qualitatively in the literature, but I have nowhere found quantitative studies aside from some experiments on mineral cycling at Oak Ridge, Tennessee, by Reichle and collaborators (1965).

One possible influence of a chemical nature was suggested by O.F. Cook in 1911, but not apparently considered by anyone subsequently. Cook, who was by profession an agricultural botanist, believed that the allomones produced by many millipeds were capable of altering soil composition by precipitating colloidal substances in the humus. He claimed, from personal observations, that "... African forests have very slight superficial accumulation of dead leaves and humus. The soil remains relatively open and noncolloidal, and is inhabited by numerous species of millipeds. In the forests of tropical America ... the underlying soils are generally much more colloidal than in Africa and the milliped population is generally sparse, or often lacking altogether ...". I pretend no knowledge whatever of this aspect of soil structure and present Cook's views here solely to give them circulation.

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RECENT ADVANCES AND FUTURE NEEDS IN THE STUDY OF COLLEMBOLA BIOLOGY AND SYSTEMATICS

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ABSTRACT

Some new results from studies of collembolan feeding, reproduction, behaviour and response to chemical pollution and mechanical habitat disturbance are presented. Morphological variation in terms of ecomorphosis, cyclomorphosis and epitoky is discussed. A future expansion into the fields of cytogenetics, physiology and functional morphology is expected to accelerate taxonomic refinement of current systematics.

RÉSUMÉ

L'auteur présente des données nouvelles sur l'alimentation des Collembolés, leur reproduction, leur comportement et leur réaction à la pollution chimique et aux perturbations mécaniques de leur habitat. Il discute de variation morphologique en termes d'ecomorphose, de cyclomorphose et d'épitokie. L'expansion éventuelle dans les domaines de la cytogénétique, de la physiologie et de la morphologie fonctionnelle devrait accélérer le raffinement taxonomique de la systématique actuelle.

BIOLOGY

Introduction

As one of the major groups of soil microarthropods, Collembola has received increasing attention from ecologists and biologists during the few last decades. Collembola biology has become a very complex and multifaceted field of research. It is impossible in just a few pages to outline all aspects of current Collembola biology studies. Instead, I will select a few important aspects of Collembola life such as feeding, reproduction, behaviour, reactions to chemical pollution and dependence on moisture - probably the one external factor that has the greatest effect on Collembolan life.

Feeding and nutrition

Apart from a few predaceous species, most Collembola feed upon a variety of organic material, both detritus and living substances, such as algae, fungal hyphae and bacteria. A considerable amount of inorganic material may pass through the digestive tract as well. Some authors regard soil Collembola as rather generalized feeders (Anderson & Healey, 1972; Greenslade & Greenslade, 1983). Others are of the opinion that they are more or less selective (Hale 1967). In either event, certain food preferences - depending on species, habitat and time of the year - are frequently reported (McMillan 1975, Vegter 1983). The coexistence of 15-20 species of Collembola in a small volume of soil may indicate that either there is a surplus of food, or that the food is partitioned by subject or by microhabitat differentiation of the involved species. The latter is obviously possible. Even a few centimeters of a soil profile is rarely uniform from top to bottom, offering a variety of habitats. But it is more difficult to explain

how nine different species of surface active *Isotoma* could occur together in a handful of damp tundra soil in north Alaska, unless there is some kind of food specialization or an excess of food (Fjellberg, unpubl.)

The uniformity of the mouthparts in large groups of Collembola has been interpreted as an indication of unspecialized feeding (Greenslade & Greenslade, 1983). However, I think this is an oversimplification. Although built around the same model, the actual construction of individual parts of the feeding apparatus varies considerably, even in close systematic groups (Fjellberg, 1984a, 1984b). And what else other than food or feeding specialization could lie behind this quick adaptive evolution? Or, to put it another way: if two related species shared the same food, why should they differentiate their feeding apparatus? I believe we still have a very crude impression of how and on what individual Collembola species feed in natural habitats, and how they interact with other members of the community. It is a great challenge to students of functional morphology and to persons who want to develop techniques for studying Collembola feeding both in laboratory and in nature.

Reproduction

As soon as the individual can keep itself alive by feeding, it must keep the species alive by reproduction. In understanding the reproductive biology of Collembola, we need information about life cycles, recruitment, mortality and other parameters. The size distribution of individuals in field populations - measured at various times during the year - has been used for a long time to obtain basic information about life cycles under natural conditions (Agrell, 1941; Fjellberg, 1975; Addison, 1981). A closer demographic analysis, involving some mathematical modelling, may also provide information about recruitment and mortality, which are essential factors in the energy budget of a population (Hale, 1980; Straalen, 1982, 1983). Data about fecundity, the potential number of eggs produced by a female, has accumulated from a number of laboratory studies. From these studies, individual fecundity appears to be rather flexible, influenced by population density (crowding), age of the individual, temperature, substrate, and other things (Hutson 1978, Snider 1973, Snider 1983). Concerning life cycles and longevity, it is clear that the long arctic winter arrests development and delays reproduction until individuals are 1-2 years old (Fjellberg 1975, Burn 1981, Addison 1977, 1981). Mature specimens may live for several (3-7) years and may reproduce several times. A winter diapause is demonstrated in several species, and is supposed to be essential for synchronization of the spring reproduction of adults in the European species *Hypogastrura socialis* (Uzel). This species has a rather fixed reproductive pattern. Adults reproduce only once in spring, and die shortly after. Pheromones appear to be essential for the group behaviour of this species (see later) (Leinaas, 1983b).

Collembola living in cold environments have clearly adopted an opportunistic reproductive strategy. Overwintering may occur in any stage of development and life cycles are adjusted to physical conditions of the habitat, which sometimes gives different life cycles in different cohorts of the population (Addison, 1977) or in different populations along a microclimatic gradient (Tamara & Mihara, 1977).

In temperate and warmer regions the generation time is shorter and reproduction runs more freely, giving a very complex age structure with indistinct cohorts (Petersen 1980, Tanaka 1970).

Behaviour

The study of behaviour and behavioural ecology of Collembola will probably receive increased attention in the future. At first consideration, the behaviour of a springtail may seem odd and bizarre. However, with closer inspection, we usually find that the behaviour is very reasonable and part of the solution to fundamental biological or ecological problems. Bretfeld (1970, 1971, 1976a, 1976b) described the rather complex mating systems and sexual interference in different species of sminthurids. Although the Collembola do not have a direct copulation and sperm transfer, the mating behaviour is probably part of the isolating mechanisms between species, just as in other groups of arthropods.

The mass occurrence of Collembola - especially on snow - is frequently noted. Less often seen, but probably of greater significance, is the aggregated occurrence of Collembola in soil and litter, where they sometimes form dense colonies of millions of individuals. We have now gained some insight into the mechanisms regulating this particular behaviour. Verhoef *et al.* (1977) and Mertens & Bourgoigne (1977) reported aggregation pheromones in Collembola. Leinaas (1983b) found a strong dependence on pheromones and phototaxis in the activity of two species of *Hypogastrura*. Leinaas & Fjellberg (1984) found a strict sun orientation in migrating colonies of an alpine *Vertagopus* species in Norway.

The social behaviour, resulting in smaller or larger aggregates, is partly interpreted as an adaptation to patchy, ephemeral habitats (Leinaas, 1983b), or - to put it in other words - to the non-random distribution of food, optimal moisture conditions, breeding sites, overwintering sites, *etc.* Obviously, pheromones help to keep the colonies together in favourable spots, as well as to coordinate their movements when they have to leave the area.

Curious enough, the mass occurrence on snow often results from the disintegration of colonies living on ground in the snow-free period. Activity on the snow surface probably acts as a way of dispersal in species that feed and breed in island-like habitats such as tree trunks, compost heaps, *etc.* A number of these "snow-flcas" also have a special winter morph with modification that possibly makes movement on the snow easier (Leinaas, 1983a).

Dependence on moisture

Moisture is probably one of the most important factors influencing the daily life of the Collembola. Unlike many other arthropods, Collembola have no hard exoskeleton that prevents evaporation from the body surface. Much research has been done on the water balance of Collembola, stressing the importance of keeping down the loss of water vapour from the body surface. Two different strategies seem to be followed. (1). Either the Collembola live in a constantly damp environment like deep soil or in caves, which makes special adaptations to dry air unnecessary. Some species of this group have completely lost their ability to control water loss (Vannier, 1977). (2). Some species have a variety of morphological adaptations to reduce the transpiration from the body surface, like scales and dense cover of hairs. This is combined in many species with an ability to actually survive shorter or longer periods with reduced water content of the body. In dry periods the species *Xenylla maritima* and *Vertagopus westerlundii* become visibly "shrunken", but are still active (Leinaas & Fjellberg, 1984). An extreme example is the inactive but reversible anhydrobiotic stage reported from several species in the Mediterranean region (Poinsot, 1968, 1974). This anhydrobiosis is also combined with the ability to survive extreme cold, as much as -180° below zero (Poinsot-Balaguer & Barra, 1983). But so far no arctic species has been demonstrated to switch to this mode of surviving the winter.

Some species have behavioural adaptations, regulating their activity to times with high substrate moisture (Leinaas & Fjellberg, 1984). Certain xerophilic species react the other way, seeking drier places when substrate becomes too damp (Vegter, 1983; Bauer, 1979).

Effects of pollution and human activities

Increased attention is paid to the ability of Collembola to live in a polluted environment. Detoxification mechanisms are found in several soil dwelling groups, like molluscs and earthworms. In Collembola certain poisonous metals are accumulated in midgut cells and leave the organism during moulting when the midgut cells are also shed (Humbert, 1974, 1977; Joosse & Bucker, 1979). Thus, the Collembola may cope with fairly high levels of metals without any immediate lethal effect. However, Joosse & Verhoef (1983) found reduced metabolic rate and lowered reproduction in Collembola which were experimentally fed on lead-contaminated food. Also Bengtsson *et al.* (1983) found reduced growth rate in the euedaphic *Onychiurus armatus* fed on Pb+Cu contaminated fungi, giving an equilibrium concentration of about 200 ppm copper in live specimens. Similar concentrations were found in a natural population of *O. armatus* in the vicinity of a brass mill. Copper is essential in respiration enzymes, and moderate levels actually increased growth rate of *O. armatus*.

A similar fertilizer effect was reported by Hågvar & Kjøndal (1981) who found an increase in density of some species in litter bags treated by simulated acid precipitation. The authors indicate a better reproductive success in "acidophile" species in litter bags with lowered pH as a possible reason for this increase.

Chemical pollution, directly affecting the physiological processes of the individual, is certainly different from the more technical disturbance of the habitat caused by activities like logging, grazing and plowing. Certain opportunistic species clearly benefit from man's activities. Greenslade & Greenslade (1983) found an increase of *r*-selected opportunistic isotomids in disturbed soils in the Solomon Islands. Unfortunately, such a faunal shift has a negative effect on the more special *K*-selected species. And these species are often stenotopic, rare and need special protection. Work in progress indicates a serious impoverishment of the endemic Collembola fauna of Hawaii (Bellinger, pers. comm.). If it is correct that arctic Collembola in general are opportunistic, as Greenslade (1983) puts it, it shall be interesting to see if they will be better off in man-made and altered habitats than their tropical relatives.

Collembolan species and assemblages have become subjects for testing ecological theories that were originally developed on vertebrates and better known groups of arthropods. I have already mentioned MacArthur & Wilson's (1967) continuum of *r*- and *K*-selection, which has now got a third dimension, the adversity or *A*-selection of Greenslade (1983) who partly used Collembola to develop the hypothesis. In future, Collembola will certainly receive increased attention from students of fundamental ecological and evolutionary processes. Such studies will probably detect and illuminate a number of taxonomic problems. And this brings me to the second part of this presentation, the systematics.

SYSTEMATICS

Introduction

The majority of collembolan taxonomists have worked in European countries. The various European schools have developed new analytical approaches to understanding structure and classification of Collembola. Consequently, the European fauna is fairly well known.

In North America, Collembola has been a much neglected group, probably because so few of them are pests in agriculture and forestry. The precise identification of North American species has been difficult due to lack of required literature. The recent, monumental work of Christiansen & Bellinger (1980, 1981) has altered this situation. However, their work is a preliminary and partly synoptic presentation of the fauna, serving as a platform for the future monographic work which is necessary. A few small soil samples from almost any part of North America will produce one or more undescribed species. Thus the North American fauna is a great challenge to taxonomists and a tremendous source of primary material for studies in classification, evolution and phylogeny. In the following paragraphs I describe some of the biological phenomena underlying the frequently observed intraspecific variation in morphology.

Ecomorphosis

The Collembola have direct development with continued growth throughout life. The various instars are separated by ecdysis in which the old cuticle is shed. Apart from the small changes related to increased size, development of hair cover and reproductive organs, more drastic changes may appear as a response to both intrinsic and external stimuli.

In a number of papers Cassagnau (1955, 1956, 1971, 1974) described ecomorphosis both in Hypogastruridae and Isotomidae. Ecomorphic specimens had enlarged setae and cuticular ridges and spines on the last abdominal segments. Also mouth parts, digestive tract and fat reservoirs of the body were affected. Ecomorphosis was supposed to be a physiological response to warm and dry conditions in species having their optimum in damp, cool, habitats. However, recent studies by Najt (1982) give a more complex interpretation. Given enough time, the classical species *Isotoma tigrina* (*olivacea* auct.) would produce ecomorphic specimens even at 5° C. Sooner or later all individuals would pass through one or more ecomorphic instars. Contrary to earlier reports, Najt also found that some of the ecomorphic specimens had normal digestive tracts and would feed. Apparently the onset of ecomorphosis is genetically fixed in the species and not a simple response to unfavourable microclimate.

Najt's observations open some very interesting perspectives. A number of isotomid genera always have abdominal spines and cuticular modifications which are essentially the same as in ecomorphic species displaying these structures in certain instars only. It seems possible that there is an evolutionary sequence from normal, "non-ecomorphic" forms to forms displaying ecomorphic traits in certain instars only (induced or not induced by external factors), to forms in which ecomorphic traits have become permanently fixed in all instars (all the "spined" isotomid genera, *Anurophorus*, *Proctostephanus*, etc.). Modifications of the digestive tract are no longer associated with this last stage, but individuals still benefit from the reduced evapotranspiration (modified cuticle) and may occupy rather xeric habitats.

Epitoky

Another phenomenon giving similar anatomical modifications as ecomorphosis, is epitoky. Epitoky is linked to the reproductive cycle and is only shown by reproductive specimens. It is quite common in many genera and affects various parts of the body, generally with reduction or modification of anal spines, claws, dens and mucro, body setae and skin granules (Bourgeois, 1971, 1973, 1974, 1981). Males of some *Vertagopus* get enlarged antennae (Fjellberg 1982).

Cyclomorphosis

A third phenomenon affecting the individual during its life cycle, is cyclomorphosis - the occurrence of seasonal forms not linked to the reproductive cycle or ecomorphosis (Fjellberg, 1976). Usually this involves the appearance of distinct summer and winter forms. Sometimes a switch from the one form to the other is associated with a shift in habitat. Certain *Hypogastrura* species have summer forms living on tree trunks while the winter forms are active on snow. The morphological changes are supposed to facilitate movement on the snow surface, and thus aid in the dispersal of the species (Leinaas, 1983a). Of particular interest are the clavate tibiotarsal hairs that appear in the European *Isotoma nivea* Schäffer during winter. Following traditional systematics, the winter form would be classified as a *Vertagopus* (Fjellberg, 1978).

Studies of the above phenomena are in an early stage. We know very little about the evolutionary significance and what it means to the individual. A number of examples are still to be detected and described. Among North American *Hypogastrura* of the *nivicola-packardinotha* groups, there are a number of forms displaying cyclomorphosis. Some of the currently recognized species are probably just seasonal forms of each other.

Chaetotaxy

In former days Collembola systematics was based on easily visible characters like number of eyes, presence/absence of certain organs, fusion of body segments, claw structures, position and shape of sensorial organs, etc. Such characters still rank among the most important, but must be used with caution as several of them are affected by the phenomena described above.

During the last two decades, several new analytical methods have come into use. One of the most promising is probably the strict use of chaetotaxy, the mapping of the body hairs. In the more primitive families of Collembola the hair cover is fairly simple and each seta has a more or less fixed position. In more advanced groups, hair cover is dense and irregular, and chaetotaxy is applied to certain parts of the body like furca, mouth region and antennae, or to "markers" like body macrochaetae or sensillae.

Chaetotaxy often provides clearcut differences among related species. Apparently evolution of the hair cover is a fairly rapid process with a high degree of parallelism even in species groups within a single genus (Fjellberg, 1984c). A general trend seems to be reduction in number and dislocation and differentiation of setae (Bourgeois & Cassagnau, 1972). Chaetotaxy as a method has developed in a rather individualistic way. Different specialists have produced more or less independent systems (Gama, 1969; Rusek, 1971; Cassagnau, 1980). An important aim for future research would be to develop a common system, making possible a comparison between distant taxa.

Cytogenetics and physiology

During the last few years, biochemical methods, cytogenetics and physiology have come into use to discriminate between species. Hale & Rowland (1977) used protein electrophoresis and amino acid chromatography and found convincing differences among forms of the problematic *Onychiurus armatus* group. Hart & Allmong (1979) made an electrophoretic analysis of esterase enzymes in species from various genera and found consistent differences. These biochemical methods are promising and may also trace populational characteristics which are not detected by traditional studies. Dalens (1982) found differences in amino acid composition in two populations of *Hypogastrura tullbergi* (Schäffer). Such differences were also

documented by studies of polytene chromosomes in *Bilobella aurantiaca* Caroli by Cassagnau (1976), Dalens (1976, 1977, 1978, 1979) and Dallai (1979). The giant chromosomes display a varying degree of polymorphism, and offer a great potential for mapping populations of different origin (Cassagnau *et al.*, 1979; Deharveng, 1982a). Even the existence of sibling species is indicated by some authors (Dallai *et al.*, 1983). Although chromosomal studies are limited to a small section of the family Neanuridae, they provide valuable information to clarify species concepts and to understand population genetics of Collembola in general.

Future approach

Sitting by the microscope to observe and make drawings is still the same approach that was used by the pioneers in Collembola systematics a hundred years ago. Although we have better quality microscopes and benefit from all the accumulated experience, the species identification of a collembolan is technically much the same as in "good old days". When the scanning electron microscope (SEM) was introduced some years ago, many people expected a revolution in the morphological studies of small organisms - of course with certain consequences to established classifications. I think it is correct to say that this has not happened in Collembola. Certainly the SEM has revealed some interesting developmental lines in surface structure of the cuticle as well as the fine structure and possible function of some sense organs. But, in routine identification and in ordinary work, the light microscope is superior.

Progress in Collembola systematics will probably not come as a result of new technical inventions - although much might happen in the fields of biochemistry and cytogenetics. There are still some parts of the collembolan body which have not - or only rarely - been used in practical identification and systematic work. The mouth region is one of the most promising. Apart from the often very complex maxillae and the simple mandibles lying inside the head, there are the external maxillary lobes, the labium, labrum and associated structures. The internal mouthparts, especially the maxilla, are commonly used in the families Neanuridae and Isotomidae, partly also Hypogastruridae (Massoud, 1967; Poinot, 1965; Fjellberg, 1977, 1984a). The labium has proved very significant in Entomobryidae and other families (Gisin, 1965; Christiansen & Bellinger, 1980; Deharveng, 1981). In a recent paper I drew attention to the maxillary outer lobe which is particularly useful in species separation in the bulky genus *Isotoma* (Fjellberg, 1984b).

As I have argued earlier I think the differentiation of the mouthparts reflects a progressive food specialization, and I believe that combined studies of structure, function and actual type of food ingested might produce some very interesting results.

In order to have success today, a taxonomist has to construct a phylogenetic tree - a cladogram. The necessary tools and methods are only partly developed in Collembola. Chaetotaxy has been used by a number of workers (Gama, 1969, 1980; Najt, 1974; Deharveng, 1982b) as well as distribution of body tubercles in Neanuridae (Cassagnau, 1983; Deharveng, 1982c). Reduction seems to be a universal principle in Collembola. Number of hairs are reduced, ocelli are lost, furca becomes shorter and finally disappears. However, several structures increase in complexity, like the feeding apparatus, the claws, the differentiation and shape of individual body hairs, and so on.

There is still a lot of work to be done before the relative plesimorphy/apomorphy of the various character states along a transformation series can be established. In order to achieve reasonably sound conclusions, it is necessary to include as many species or samples as possible from the entire geographical area covered by the taxon under study. In this context, the rich

Nearctic fauna is particularly important as a pool of still unknown or inadequately described species.

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PTERYGOTE INSECTS AND THE SOIL: THEIR DIVERSITY, THEIR EFFECTS ON SOILS AND THE PROBLEM OF SPECIES IDENTIFICATION

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ABSTRACT

Attention is focussed on soil-dwelling pterygote insects that directly influence soil profiles and soil fabrics, especially on the largest order of insects the Coleoptera or beetles, and is then further restricted to groups that are important in the tropics and in the southern hemisphere. This means especially termites (Isoptera) and ants (Hymenoptera, Formicidae). These two groups of insects affect soil structure by building mounds and excavating nest chambers and galleries, often raising lower horizon material to the surface. They also influence the nature of organic matter and its distribution in the soil profile and, consequently, the horizontal dispersion of plant nutrients. Some of these influences are illustrated by reference to recent work on the micromorphological and profile-forming effects of termites. Recent Australian studies are also used to illustrate the pedological effects of ants. In turn, Australian ants introduce, and are used to exemplify, the general taxonomic problem presented by many groups of soil-associated pterygote insects in many parts of the world: numerous species, most of which are underscribed. The magnitude of this problem is examined on a world basis and it is suggested that the conventional taxonomic process should be inverted: work should proceed downward, starting from the higher taxa, organizing the species of larger genera in natural species groups. Species-level taxonomic studies can be deferred, carried out on a provisional basis or concentrated on critical groups of species.

RÉSUMÉ

L'auteur passe en revue les groupes d'insectes ptérygotes qui habitent le sol et autres habitats semblables. Il se concentre sur ceux qui influencent directement les horizons et la structure des sols, plus particulièrement sur les Coléoptères, qui forment le plus grand ordre d'insectes; par la suite il restreint encore davantage son analyses aux groupes importants des tropiques et de l'hémisphère sud, c'est-à-dire plus spécialement les termites (Isoptères) et les fourmis (Hyménoptères, Formicidae). Ces deux groupes d'insectes affectent la structure du sol en construisant des monticules et en creusant des chambres de reproduction et des galeries, amenant ainsi à la surface des matières provenant des horizons inférieurs. Ils influencent aussi la nature de la matière organique et sa répartition dans le profil du sol et, par conséquent, la dispersion horizontale des éléments nutritifs des plantes. Quelques-uns de ces effets sont illustrés à l'aide d'exemples de travaux récents sur le mode d'influence des termites sur la micromorphologie et la formation du profil des sols. De récentes études australiennes servent aussi d'exemples pour illustrer les effets des fourmis sur les sols. De même, l'exemple des fourmis australiennes sert à illustrer le problème général d'ordre taxonomique que présentent plusieurs groupes d'insectes ptérygotes associés aux sols dans plusieurs régions du monde, c'est-à-dire la présence d'un très grand nombre d'espèces dont la grande majorité n'est pas décrite. L'auteur analyse l'ampleur de ce problème à l'échelle mondiale et conclut que le processus conventionnel de la taxonomie devrait être inversé: c'est-à-dire que les travaux devraient progresser du général au particulier, en étudiant d'abord les taxons supérieurs et en divisant les gros genres en groupements naturels d'espèces. Quant aux traitements taxonomiques des espèces, ils peuvent être soit retardés, soit exécutés de façon provisoire, ou encore concentrés sur des groupes d'espèces

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critiques.

INTRODUCTION

The subclass Pterygota consists of insects which, as adults, are winged or are secondarily apterous. The subclass contains about three-quarters of all the described species of animals and a very substantial proportion of them are associated with the soil system. This refers to the actual mineral and organic horizons of the soil profile and also to related decomposition habitats such as decaying wood and fallen fruits, carrion and dung. Conventionally regarded as soil animals as well are those that are active on the soil surface, among insects for example, many carabid beetles and ants. Indeed it is at the air-soil interface *i.e.*, the soil surface and uppermost part of the soil profile, that biological activity and diversity usually reach their absolute maxima in terrestrial ecosystems. Much of this diversity, both taxonomic diversity and diversity of form and function, is due to pterygote insects. This account of pterygote-soil relationships is inevitably cursory, even with several restrictions of the area which I attempt to cover. In accordance with the subject of the Symposium, attention is concentrated on those pterygote groups that influence soil fabrics and the constitution of soil profiles. Until recent years, by far the greater part of research in soil zoology had been carried out in temperate regions in the northern hemisphere. Here, therefore, as a gesture towards restoring some balance, and to complement other contributions to this volume, I emphasize two groups, termites and ants, that are particularly important in soils throughout the tropics and over much of the southern hemisphere. I also select out the Coleoptera or beetles, by far the largest order of insects and whose species interact with the soil in a multitude of different ways.

THE VARIETY OF SOIL PTERYGOTA

Of the 26 orders that form the Pterygota all but seven contain at least some species in which an active life history stage involves or depends directly on the soil system. The Phasmatodea (stick insects) live and feed on vegetation (although the eggs are deposited on or laid in the soil), while Phthiraptera (lice), Siphonaptera (fleas) and Strepsiptera are parasitic. Three other orders have winged, generally short-lived adults and exclusively aquatic larvae. Similarly the Odonata (Dragonflies) and Trichoptera (caddisflies) are essentially aquatic but in both groups are a few species with truly terrestrial larvae living, for example, in rainforest litter far from standing water. Increasing terrestriality is seen in the Mecoptera (scorpion flies); the larvae are mainly aquatic or are found in damp swampy habitats but some are predators and scavengers on the open soil surface and in litter.

The other 16 orders are of varying importance in the soil system. Zorapterans, grylloblattodeans, and embiopterans are relatively small and obscure orders and are, as a rule, of minor functional importance. Zorapterans are small (length < 3mm) gregarious insects living in logs in the tropics. Grylloblattodeans are small and are found under stones and logs, and in the soil in cold wet situations in the northern hemisphere. The mainly tropical embiopterans construct silken galleries, sometimes in leaf litter, under stones or in crevices in the soil. Mantodea (preying mantises) are primarily predators on vegetation but there are some representatives adapted to life on the soil surface.

Members of all the remaining dozen orders contribute significantly to soil processes. The Isoptera (termites) are the most closely associated with the soil and they, with the ants (Hymenoptera, Formicidae, are dealt with separately below. The activities and influences of

the rest of the Pterygota are far too varied for it to be possible here to do more than note a few salient points for most orders.

Blattodeans (cockroaches) and dermapterans (earwigs) are omnivorous feeders and detritivores. Ground-living psocopterans (booklice) and thysanopterans (thrips) feed on a wide range of unicellular algae, lichens and fungal hyphae and spores amongst litter and on the soil surface. Orthoptera (grasshoppers and crickets) include many cryptic forms that shelter in burrows in soil and decaying wood or under debris, and a smaller number of wholly subterranean species that are highly adapted morphologically to life in the soil (Key, 1970). Among the Neuroptera (lace wings) there are families whose larvae are terrestrial predators, notably the ant-lions (Myremeleontidae) some of which construct pitfall traps in loose sandy soils. The importance of Lepidoptera (butterflies and moths) as soil animals is probably underestimated. In Australia the larvae of at least six families, especially Tortricidae, feed on dead leaves in the litter layer, (Common, 1970), very often when the dry condition of these leaves inhibits attack or decomposition by other organisms, while some cossid larvae feed, internally or externally, on the roots of trees and shrubs. Ground-living Hemiptera (bugs) include seed-feeders, a wide variety of predators and fungus feeders. Some aphids and, probably, most cydnidas are root-feeders. The Diptera (flies) form one of the larger orders of insects and very many of their larvae occur in moist, nutrient-rich habitats such as decaying fruits, dung, rotting vegetation, carrion and logs which have a large active microbial population at a moderately advanced stage of decomposition. Some of these larvae are predaceous and many others have more or less specialised relationships with fungi.

A more detailed examination of the remaining order, the Coleoptera (beetles), which contains about 40% of all known insect species and perhaps a third, or even more, of all animal species, illustrates the taxonomic complexity of pterygotes associated with the soil. In Table 1 the families of Coleoptera are arranged in four groups. Group 1 consists of families composed of species that can be regarded as effectively independent of the soil both as adults and larvae. It covers parasites, aquatic forms, species living entirely on vegetation or in the nests of vertebrates and social insects. Group 2 includes all families that have representatives functioning in the soil system, including species whose activities are centred on discrete habitat units such as logs and vertebrate dung and carrion. Group 3 excludes the latter and is restricted to families with species living in soil or litter or on the soil surface. Group 4 is further restricted to families containing species that penetrate the soil profile and are therefore likely to affect soil properties directly. Table 1 is derived from a summary of the classification of Coleoptera given by Britton (1970) modified according to subsequent major changes (Britton, 1974). This classification is essentially that of Crowson (1955, 1967) and it was used also by Richards and Davies (1960) who provide brief notes on the biology of the families. Several points should be noted. The Table refers to species of Coleoptera known in 1970. By 1974 the total had risen from about 280,000 species to 290,000 (Britton, 1974). If this represents a steady rate of increase, the total should now stand at around 320,000 known species. However this must still fall very far short of the real total of all species of Coleoptera (see below). Inevitably the attribution to categories 1-4 in the Table is arbitrary and debatable for many taxa. Families are placed according to whether they contain representatives in the habitat groups 1-4. The Carabidae for example are in Group 4 because the family contains species with burrowing adults while the larvae of many species with surface-active adults live in the upper part of the soil profile. This does not mean however that all Carabidae fall in Group 4 and indeed there are many highly adapted arboreal carabid species, especially in tropical rain-forests. It does mean

TABLE 1. Degree of association of families of Coleoptera with soil and allied habitats. The Table shows the number of known species in families which contain representatives variously associated with the soil. Only the major families ($> 2,000$ known species) are shown individually; the fractions represent number of families/number of known species (see text).

Superfamily	Habitat				Totals
Family	1 Unrelated to soil (or uncertain)	2 Soil System	3 Ground layer	4 Soil profile	
Cupedoidea	—	2/26	—	—	2/26
Sphaerioidea	4/22	—	—	—	4/22
Caraboidea					8/30,184
Carabidae	—	1/25,000	1/25,000	1/25,000	
Other families	6/5,059	1/125	—	—	
Hydrophiloidea					5/2,400
Hydrophilidae	—	1/2,000	—	—	
Other families	4/400	—	—	—	
Histeroidea					3/2,507
Histeridae	—	1/2,500	—	—	
Other families	—	2/7	—	—	
Staphylinoidea					10/35,149
Staphylinidae	—	1/27,000	1/27,000	—	
Pselaphidae	—	1/5,000	1/5,000	—	
Other families	3/49	5/3,100	4/2,800	—	
Scarabaeoidea					6/18,827
Scarabaeidae	—	1/17,000	1/17,000	1/17,000	
Other families	—	5/1,287	3/1,587	1/300	
Eucinetoidae	1/360	2/85	1/61	—	3/445
Dascilloidea	1/50	2/69	2/69	1/65	3/119
Byrrhoidea	—	2/300	1/270	—	2/300
Dryopoidea	7/1,008	—	—	—	7/1,008
Buprestoidea					1/11,500
Buprestidae	—	1/11,500	—	—	
Artemetopoidea	1/45	2/115	1/1	—	3/160
Elateroidea					5/8,208
Elateridae	—	1/7,000	1/7,000	1/7,000	
Other families	—	4/1,208	1/3	—	
Cantharoidea					7/8,252
Lycidae	—	1/3,000	1/3,000	1/3,000	
Cantharidae	—	1/3,500	1/3,500	—	
Other families	1/3	4/1,749	4/1,749	—	
Dermestoidea	3/88	1/731	—	—	4/819

(continued on next page)

Table 1 (continued)

Superfamily	Habitat				Totals
Family	1 Unrelated to soil (or uncertain)	2 Soil System	3 Ground layer	4 Soil profile	
Bostrychoidea	1/700	3/1,604	1/70	1/70	4/2,304
Cleroidea					7/9,152
Cleridae	—	1/3,400	—	—	
Melyridae	—	1/4,000	1/4,000	1/4,000	
Other families	1/3	4/1,749	4/1,749	—	
Lymexyloidea	—	1/37	—	—	1/37
Cucujoidea					46/41,011
Nitidulidae	—	1/2,200	1/2,200	—	
Coccinellidae	1/5,000	—	—	—	
Meloidae	1/2,000	—	—	—	
Tenebrionidae	—	1/16,100	1/16,100	—	
Other families	16/2,702	26/13,009	8/8,087	—	
Chrysomeloidea					3/41,200
Cerambycidae	—	1/20,000	1/20,000	1/20,000	
Chrysomelidae	—	1/20,000	1/20,000	1/20,000	
Other families	1/1,200	—	—	—	
Curculionoidea					8/61,264
Anthribidae	—	1/2,400	—	—	
Curculionidae	—	1/60,000	1/60,000	1/60,000	
Other families	4/514	2/1,350	—	1/1,060	
Totals	56/19,200	86/258,621	43/225,857	12/137,495	142/282,880

that identification of a carabid species from soil entails its discrimination within a family of more than 20,000 known species.

The functional complexity of soil-associated Coleoptera has to be considered as well. The very high proportion of families in Group 2 in Table 1, and the large number of known species in these families (over a quarter of a million) reflects, in part, the close association of Coleoptera with dead wood and fungi. For example, many Coleoptera have mycangia, structures that allow adult beetles to transport fungal spores when they move from one site to another. The superfamily Cucujoidea is particularly well represented in Group 2. It is conservatively divided into 45 families but well over 50 can be recognised, ranging from the Tenebrionidae, a major family of important detritivores, especially in the tropics and

TABLE 2. Summary of the superfamily Scarabaeoidea (Coleoptera): larval habitats and food

Family Subfamily	Known species (1970)	Larval habitat	Food
Lucanidae	750	Dead trees, logs, stumps	Decaying wood
Passalidae	490	Under bark of dead trees, in logs	Decaying wood
Geotrupidae	300	Soil, often in excavations below dung	Dung, fungi, green and decaying vegetation
Acanthoceridae	120	? Under bark, in litter, soil	? Decaying vegetation
Trogidae	167	Soil below dry vertebrate carcasses	Carrion
Scarabaeidae			
Aclopininae	14	?	?
Hybosorinae	100	Ground layer	Carrion
Aphodiinae ¹	1,220	Dung, or burrows in soil	Dung, green vegetation at night, ? roots
Scarabaeinae	2,000	Soil below dung	Dung
Melolonthinae	9,000	Soil	Roots, organic matter
Rutelinae	2,500	Soil	Roots, organic matter
Dynastinae	1,400	Soil, logs	Roots, organic matter
Valginae	200	? Associated with termites	
Cetoniinae	2,600	Soil, humus	Organic matter

¹ Including Aegialinae

subtropics, to numerous smaller families of small beetles, many of which probably have very specialised relationships with micro-organisms.

Even if attention is restricted to Group 4 in Table 1 there still remains the majority of the larger families of Coleoptera, *i.e.*, six families of 7,000 to 60,000 known species. Apart from their mechanical effects on soils they are important as predators of other soil animals, or as feeders on roots, dead plant material and/or associated microbial biomass. The Carabidae, which have been mentioned, are predominantly predators and scavengers while the larvae of many if not most Elateridae are root-feeders. Although Cerambycidae, Chrysomelidae and Curculionidae are all typically phytophagous above the soil surface, the Cerambycidae and Curculionidae (the largest family of animals) contain root-feeding species. In the Chrysomelidae, larvae of Eumolpinae and Cryptocephalinae are found in the soil and, they probably feed on roots as well.

Finally the Scarabaeidae and other families in the Scarabaeoidea exemplify a single major phylogenetic radiation which contributes to the soil, and to the soil system as a whole, in a variety of different ways. The larvae live almost exclusively in soil and allied habitats (Table 2) and occupy a low position in the trophic system, feeding mainly on live and dead plant material and associated micro-organisms. Adult scarabaeoids are large bulky beetles, up to 7.5 cm or

more in length and the group includes some of the largest of all insects. They can occur at very high population densities, for example around 400 scarabaeids per square metre in Australian and New Zealand grasslands. Without entering into the extensive literature on their population dynamics and pest status, it can be noted that Scarabaeidae in particular can have important influences on soil properties and processes. Over much of the Old World tropics and subtropics they also have a very significant role in nutrient cycling by disposing of large quantities of dung produced by herbivorous mammals (Bornemissza, 1961). This may be consumed by the larvae on the soil surface or in burrows excavated and stocked by the parent beetles.

The question of the food of larval scarabaeoids typifies a recurrent problem in soil zoology: to distinguish between what is ingested and what is digested. Scarabaeid larvae for instance commonly ingest live and dead roots, soil organic matter, mineral particles of the rhizosphere and other micro-organisms; for any one scarabaeid species it may be difficult to establish on what elements of this intake larval nutrition actually depends (Greenslade and Greenslade, 1983). This is complicated by the existence of a continuum, in the Scarabaeidae for example, from Cetoniinae whose larvae feed on organic matter, to Rutelinae and Melolonthinae feeding on live roots. The digestive physiology of scarabaeoid larvae is an important topic which is beyond the scope of this paper but, clearly, the group as a whole is one which merits much more attention from the point of view of their effect on the soil system (see Table 3 below).

PEDOLOGICAL INFLUENCES OF SOIL PTERYGOTA

Hole (1981) discussed 11 different ways in which animals can affect soils citing many examples, with references, that involve insects. They need not be repeated here in detail but three groups are briefly examined (Table 3).

Merely by excavating galleries and burrows in soil all three of the taxa in Table 3 contribute to effects 1, 2, 4 and 6. Humphreys and Mitchell (1983) suggest that mixing by soil animals may have a significant effect on the rate of development of texture contrast soil profiles; they point out that, over time, it allows rainfall to affect a greater thickness of the profile than just the surface. Ants and termites backfill voids (effect 3) when they remodel their nests or when those structures are taken over and altered by other ant or termite species, and soil-living scarabaeid larvae generally fill their burrows behind them. Soil erosion (effect 5) is influenced by removal of plant-cover (e.g., by scarabaeoid larvae) and by deposition of loose soil on the surface, susceptible to movement by wind or water, when subterranean nests are initially excavated or when they are cleaned (e.g., by ants). Elevated ant and termite mounds with a cemented surface or matrix, or a protective gravel cover can reduce erosion locally but may accelerate it elsewhere by modifying surface run-off of rain water.

Because of their population biomass and their food, ranging from dry dead wood to already well-decomposed organic matter, both termites and scarabaeoids have important influences in regulating the nature and mass of plant litter, and the course and rate of decomposition and hence nutrient cycling (effects 7 and 9). Termites can accelerate processes by disposing of recalcitrant substances with a high content of lignin, or retard them by locking up material in long-lasting nest structures (Lee and Wood, 1971). Ants have minor effects here although those with large thatched mounds, for example some wood ants, *Formica* spp. in the northern hemisphere, and the myrmicine *Myremecia pilosula* in Australia, have some effect on the distribution of litter. However, Cowan *et al.* (1985) concluded that the Australian *Camponotus intrepidus* which also has thatched mounds, has a trivial role in pedogenesis. Ants very rapidly

TABLE 3. Pedological effects of soil fauna, from Hole (1981), and the roles of the pterygote insects: termites, ants and scarabaeoid beetles.

Effect		Taxon		
		Termites	Ants	Scarabaeoids
1.	Mixing	+	+	+
2.	Forming voids	+	+	+
3.	Backfilling voids	+	+	+
4.	Forming and destroying peds	+	+	+
5.	Regulating soil erosion	+	+	+
6.	Regulating movement of water and air in soil	+	+	+
7.	Regulating plant litter	+	(+)	+
8.	Regulating animal litter	+	+	+
9.	Regulating nutrient cycling	+	(+)	+
10.	Regulating biota	-	+	+
11.	Producing special constituents	+	+	+

recycle any invertebrate carrion that appears on the soil surface (effect 9) usually finding it within minutes of its arrival, but this cannot compare with the mass effect of termites and beetles (such as scarabaeoids) on plant material.

Termites seem to have little direct influence on other biota (effect 10), excluding their microbial gut flora and the animals, mainly insects, that live with them in their nests. Indeed much of the success of the order Isoptera must derive from their exploitation of resources that were hardly used by other animals. In contrast, ants are particularly significant as dominant predators and competitors on the soil surface and in litter, with profound effects on the rest of the soil and surface fauna at both ecological and evolutionary levels. Soil-living scarabaeoids perhaps illustrate the classic influences of soil fauna (according to conventional wisdom) in comminuting plant material, dispersing soil micro-organisms and controlling their populations by feeding upon them.

All three taxa have the final effect (11) of producing special constituents. Both ants and termites make structures from selected soil particles, frequently cemented with salivary secretions or faecal material, while scarabaeoid larvae leave excreta-filled tunnels behind them.

Three effects of soil insects do not come across clearly in Hole's scheme. They are effects: (1), on the rhizosphere (*e.g.*, by scarabaeoid larvae); (2), of soil-nesting and mound-building ants and termites on the distribution pattern of plant nutrients in the horizontal plane; and (3), on the composition and structure of A-horizons (although to some extent the last is covered by Hole's 'mixing' or 'bioturbation').

The interactions of termites with soils were reviewed by Lee and Wood (1971). They showed that two of the most important activities of species that build mounds are the concentration, in the mounds, of organic matter and hence plant nutrients, and the elevation of lower horizon

material to the surface. More recently, Holt *et al.* (1980) and Spain *et al.* (1983) have studied the pedological significance of mound-building termites in northern Australia and their results are typical of those in the literature. On two soil types (red and yellow earths) Holt *et al.* (1980) found a total mound basal area of about 1% of their plots. Assuming the life-time of a mound from inception to complete erosion to be 25–50 years, they calculated an annual rate of accumulation of lower horizon soil on the surface of 0.025–0.05 mm per year. This means that any point in the landscape will support a termite mound once every 1–1,000 years and that in the 10,000 years since the end of the Pleistocene a 20–50 cm thick uppermost horizon could develop from the erosion of termite mounds. Since termite galleries commonly extend 1–2 m into the soil it follows also that over a few millennia entire soil profiles, or all of the upper part, can be worked and reworked by termites. In this way, termites appear to have a major role in the formation of the tubulo-alveolar laterites and pisolitic laterites and bauxites that are frequent throughout the warmer parts of the world. From the micromorphology of these laterites and bauxites, and their content of plant and termite fragments, de Barros Machado (1982a, b) concluded that they are formed by capillary impregnation by sesquioxides of the lining of termite galleries.

Mound-building ants also have received considerable attention on account of their possible role in raising soil to the surface and in affecting the distribution of plant nutrients, recently for example from Briesse (1982), Cowan *et al.* (1985), Culver and Beattie (1983), Davidson and Morton (1981), Humphreys and Mitchell (1983) and Mandel and Sorenson (1982) and these authors provide many references to earlier investigations. Most of this work however has been done outside the tropics (in which ants reach their greatest diversity) and has generally involved only one or a few ant species which construct distinct nest mounds.

Humphreys and Mitchell (1983) recognised two broad types of mound, Type I where subsoil material is simply deposited loosely on the surface and Type II in which the mound is chambered, and the material compacted and cemented, to form a much more permanent nest structure. In fact there is a continuous range of nest types from subterranean nests that just open on to the soil surface, to entrances that are surrounded by fans, rings or small turrets of loose soil, through mounds that are increasingly compacted, worked and variously covered with thatch or gravel, to some very elaborate structures. Examples are the nests of New World fungus-growing ants (Attini), described by Moser (1963) and Weber (1966) (and see Wilson, 1971), and the ring nests of certain *Polyrachis* species on red earths and earthy sands in central Australia. The latter, which have yet to be described in detail, consist of substantial earthen rings which are covered with dead leaves of mulga (*Acacia aneura*) and contain a complex arrangement of interpenetrating galleries and spouts opening into voluminous atria.

These mound structures have a variety of functions ranging from spoil heaps or middens, to the control of nest microclimate and flood-defence. When they are thatched or covered with gravel the covering may act as a protection against rain splash erosion (Cowan *et al.*, 1985) and/or as a behavioural boundary (Gordon, 1984).

For some species the longevity of these mounds, for example the large gravel-covered nests of the meat ant, *Iridomyrmex purpureus*, of eastern Australia, is such that their contribution to pedogenesis is negligible, despite their size (Greenslade, 1974; Cowan *et al.*, 1985). In other species, however, the turnover rate is much more rapid and Culver and Beattie (1983) cite King and Sallee's (1956) and Smallwood's (1982) observations that the half life of large *Formica* mounds may be 10 years or less while some species relocate their nests several times a year. In arid Australia there are indications that nest turnover, even for the elaborate ring nests of

Polyrachis species, is very much more rapid than was hitherto assumed (P.J.M. Greenslade and W.A. Low, E. and B. Case, unpublished observations). It has been estimated that subsoil is brought to the surface by ants at rates of up to 0.1 mm per year, for example by *Formica cinerea* in North America (Baxter and Hole, 1967), quite comparable with estimates obtained for termites. These rates are of a magnitude that could be a significant influence in pedogenesis within the time-span of the Holocene so that it becomes unnecessary to extrapolate over longer periods of time that include major climatic changes and probable changes in the rate and nature of biological activities in the soil. Humphreys and Mitchell (1983) point out that, depending on soil material, rate and depth of mixing, and intensity of rainfall and rainwash, animal activity in general (including that of ants and termites) can either homogenize soil profiles or accentuate texture contrasts, leading to duplex profiles.

In semi-arid southern Australia Brieese (1982) studied the combined effects of the members of a moderately diverse assemblage of ants. There was a total of 22 species in a plot of 500m² of low, open chenopod shrubland and none of them built large mounds. The turnover rate of soil attributed to these ants was 0.03 mm a year, again comparable to figures for termites in northern Australia.

Several investigators have compared the properties of mound and nonmound soils [see for example Culver and Beattie (1983), Davidson and Morton (1981a, b) Mandel and Sorenson (1982)]. They found commonly, but not invariably, enhanced levels of plant nutrients in the mound soils, notably of nitrogen and available phosphorus and, where ants allow plants to grow on mounds, floristic contrasts with surrounding areas. Brieese (1982) compared soils from the nests of six selected ant species with those from control sites. Four seed-harvester or seed-harvester-omnivore species and one predator showed increased concentrations of nitrogen and phosphorus in nest over control soils, especially close to the surface. This was related to the presence of discarded prey fragments, seed husks and other plant material. However, a non-harvesting ant, an *Iridomyrmex* species which is a predator-omnivore, does not discard material around the nest entrance, and there was no nest-enhancement of plant nutrient concentrations. Levels actually decreased, probably because of the presence of lower horizon material that had been brought to the surface.

Charley (1971) and Rixon (1970) have described and discussed the significance of the surface patterning of plant nutrients in the type of shrubland in which Brieese studied ants. Brieese added the point that, by concentrating nutrients around their nest entrances, ants contribute to a mineral mosaic which influences the overall nutrition of the plant community. This can be extended to other soil-nesting ants and termites. The scale at which they are likely to influence nutrient patterns is close to that illustrated by Tillman (1982), who argued that adaptation to and competition for specific ratios of resources, such as nutrients, is a major factor in the coexistence of plant species and in the control of floristic diversity. Consequently, the effects of social insects on soils may have wide significance to vegetation.

Brieese's (1982) work takes us back to the problems created by insect diversity. First, when ant communities are composed of large numbers of species (as is the rule over most of Australia for example, and the whole of the world's tropical regions) with differing effects on the soil, the influence of each species should be assessed independently. When a local ant fauna can consist of more than 100 species in an area of less than 1 ha, the difficulties are obvious. Second, there is the problem of identifying the species, essential if one study is to be comparable with another.

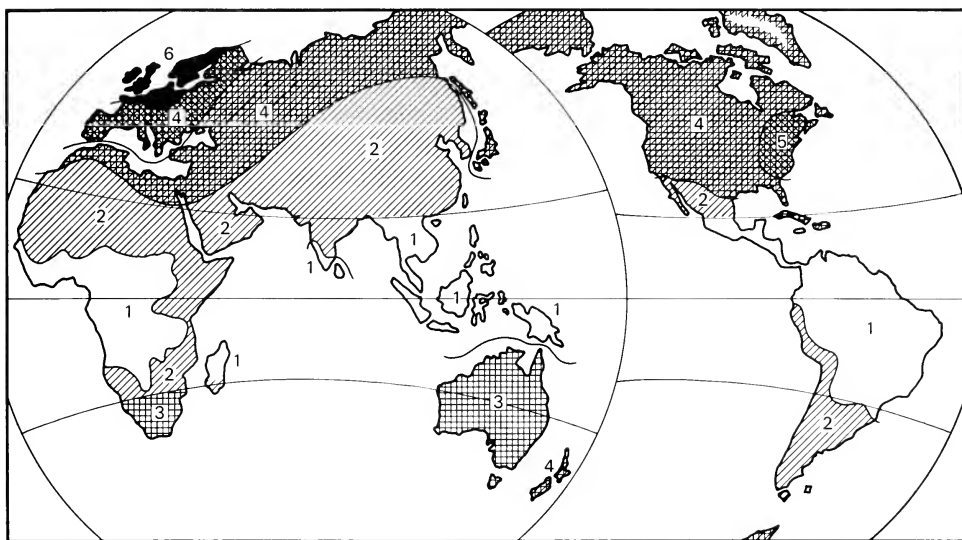


Fig. 1. Relative apparent taxonomic knowledge of soil Pterygota, from 1, probably very inadequate for most groups, to 6, good, more than 90% of species described, at least as adults, in most groups.

IDENTIFICATION OF SOIL INSECTS

The accurate identification of species is essential to any biological study in order to allow the comparison, application and testing of results, just as the consistent and accurate identification of soil types is essential to any study of soils. Hollis (1980) has edited a multi-authored guide aiming to provide a list of primary references, enabling non-specialists to set about identifying insects, including soil pterygotes, from any part of the world. Because of the diversity of soil biota, however, and especially of soil insects, specific identification often seems to be an ideal the attainment of which is surrounded by insuperable barriers. In many studies, specific identification is sacrificed for the sake of statistical validity, and animals identified only to the level of the family or even the order, a pronounced deficiency of much research in soil zoology.

Australian ants illustrate the sort of problem that the identification of insect species presents to the soil zoologist. To take only one example, Bolton (1981) revised the African members of the ant genus *Meranoplus* which is distributed through the Old World tropics and adjacent areas. From the taxonomic literature, he concluded that the Australian region had the most diverse fauna with *ca.* 25 named taxa. Since 1970, I have collected more than 200 *Meranoplus* species in Australia and this can be but a fraction of the total so that less, and probably much less, than 10% are described. Consequently, for this quite important genus there are hardly any descriptions of species, no keys for their identification and its study is closed to the non-specialist. Admittedly, the Australian ant fauna is remarkably diverse; but in other continental areas other groups of soil insects have radiated in the same way, creating the same obstacles to research.

New (1984) refers to this as the 'taxonomic impediment' to work on insects. The problem was discussed by Wilson (1980) who considered it capable of being solved. He started with the then commonly agreed maximum figure of a total of 10 million species of organisms of which *ca.* 1.5 million had been described. He suggested that if a taxonomist deals with 10 species per

year over a span of 40 years, 25,000 taxonomists' working lives would be required to revise the biota of the world, a not impossible number given contemporary populations of scientists. However, basing calculations on the number of host-specific Coleoptera on tropical trees, Erwin (1982) proposed that there may be up to 30 million species of tropical arthropods. New (1984) describes "reactions ranging from incredulity to relief that a more realistic figure has been published." It is unlikely that many soil zoologists acquainted with the invertebrate fauna of the litter layer in lowland tropical rain-forests would dispute Erwin's estimate, even if they disagreed with the means by which he arrived at it. Indeed it is quite probable that an extensive survey of ground-layer invertebrates in tropical rain-forests would result in another massive increase to the estimated total. It should be added that this figure refers to taxonomist's morphological species and evades the question of species that can be recognised only with the biochemical and karyological techniques of the geneticist.

The taxonomic problem is not uniformly spread throughout the different groups of soil insects or the world's geographical regions. Some insects that are important in the soil system are relatively well known, even in the tropics. The prime example is the Isoptera (termites) although even here much taxonomic study is still needed. At the other extreme lie groups such as tropical curculionid and staphylinid beetles. There have been a number of attempts to assess the state of taxonomic knowledge of selected portions of the biota. Examples are surveys of recorded, and estimates of the uncollected, soil fauna of Canada (Danks, 1979; Marshall *et al.*, 1982); terrestrial and freshwater Hexapoda (*i.e.*, pterygote and apterygote insects and allied groups); Myriapoda and Arachnida of New Zealand (Watt, 1983); insects of Australia (Taylor, 1976); and biota of the British Isles with particular references to insects (Stubbs, 1982). Figure 1 is a very subjective attempt to illustrate geographical variation in the apparent magnitude of the taxonomic impediment to work on the pterygote of the soil insects. It derives from surveys such as those mentioned, superficial familiarity with the taxonomic literature and the impression gained from collecting and sampling a variety of soil insects in the world's major biomes. Regional variation is caused by such factors as differences in the diversity of faunas and in the history of biological investigation in different areas.

By far, the best known soil insects are those of Britain and northwestern Europe, where probably more than 95% of species are described and a comprehensive range of guides and keys to adults is available. Even here, however, the specific identification of immature stages is generally difficult and impossible for many taxa. In New Zealand, more than half the species are thought to be described, while in Australia, it is estimated that more than half have yet to be collected. In the humid tropics, of course, the situation is much worse, but precisely how much we do not know.

Much current taxonomic work is based on revisions of genera, in which all available representatives of a genus are gathered together and species are described or redescribed and catalogued. It is then possible to revise the higher classification and to prepare keys to species. For most of the world's soil pterygotes it is obvious that this conventional taxonomic process is quite inadequate. For example, of the postulated 30 million or so arthropod species about 12 million or 40% should be Coleoptera. At the current rate at which Coleoptera species are being described (*ca.* 2–3,000 per year, see account of Coleoptera here) a very long time indeed would elapse before all were known. Unsatisfactory partial answers are available in that attention can be restricted to better known taxa and/or the soil zoologist can become his own taxonomist. Sometimes species can be identified through a combination of voucher specimens and code numbers, but this system fails in large, inadequately known genera. A possible solution lies in

inverting conventional taxonomy. Instead of starting with the description of species, work should proceed downward from higher taxonomic categories in order to provide guides to genera and, within large genera, to natural groups of species. In this way, the material with which the soil zoologist works is reduced to sets of species of manageable size that are relatively easily recognised and when recognised convey biological information. It is feasible also to link species' identities to vouchers and code numbers. The time-consuming production of detailed species-descriptions, which generally fail to discriminate between sibling or cryptic species, and are rarely adequate without access to types, can probably be omitted. At least it can be deferred, carried out on a provisional basis or concentrated on critical groups of species.

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SOIL ANIMALS AND SOIL FABRIC PRODUCTION: FACTS AND PERCEPTIONS

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ABSTRACT

Soil is composed of microenvironments resulting largely from distinct biological inputs or activities. These microenvironments in turn foster development of microcommunities which, in composite, determine patterns of soil micromorphology. Biological processes contribute to the local dynamics of microcommunities, bring about changes in soil structure, and are major features of soil function. Various spheres of influence, based upon soil microcommunities organize biologically mediated interactions between soil structure and soil function.

RÉSUMÉ

Le sol se compose de microenvironnements qui résultent principalement d'énergies ou d'activités biologiques distinctes. En retour, ces microenvironnements promouvoient le développement de microcommunautés qui, dans leur ensemble, déterminent les différents aspects de la micromorphologie du sol. Les processus biologiques contribuent à la dynamique locale des microcommunautés, modifient la structure du sol, et sont parmi les plus importants aspects de la fonction du sol. Diverses sphères d'influence, qui originent des microcommunautés terricoles, organisent, par l'entremise d'agents biologiques, les actions réciproques entre la structure et la fonction du sol.

INTRODUCTION

The contribution of soil animals to production and maintenance of soil fabrics is a vital part of soil function., Being a complex system, soil must be investigated in a holistic way so as to include the influence of soil animals.

Soil litter is the major source of organic input at the interfaces with the abiotic mineral soil. Soil litter is composed of a variety of plant parts including various species of leaves, seeds and fruits, other dead plant tissues - woody and herbaceous, fungal fruiting bodies, rhizomorphs and other microbial tissues. Animal contributions to litter are of all types and sizes: fecal masses and pellets, nesting materials and various forms of shed skins, egg shells and carcasses. Litter may appear as a zone of very high entropy, but when viewed in a more microscopic sense, order abounds, and within a very short time interbiotic and biotic - abiotic organization reaches high levels of fidelity. Cybernetic information is stored and patterns become more predictable soon after litterfall. Each litter component, being of different taxonomic origin or morphological form, provides a unique mass of highly organized elements, compounds and energy sources, and is a potential microhabitat. Each type of microhabitat, dependent upon its origin or form, further supports a predictable microcommunity of associated soil organisms predominantly decomposer microorganisms and invertebrates - the decomposer food web (Dindal, 1971;

1980). Decomposer microcommunities are structurally and functionally unique (Dindal, 1971; 1978a,b). When we think of the array of litter microcommunities as intricately related to abiotic soil components, a microecosystem paradigm emerges. Furthermore, the micromorphology of the soil fabric is an expression of microcommunity structure and function. Biological mediation, therefore, is vital at interfaces within the soil, and entropy of the soil ecosystem is continually lessened by these biotic activities. The microecosystem/microcommunity concept provides an obvious link connecting the abiotic, vegetative and vertebrate animal characteristics of any macroecosystem; thus a holistic approach to the understanding of soil fabric production is imperative.

AUTUMN OF LIFE

Litter Fall

An obvious component of soil litter is the mass of deciduous leaves shed annually within a temperate forest. In a northern hardwood forest in central New York (dominated by sugar maple, *Acer saccharum* Marsh, and ash, *Fraxinus* spp.) all of the leaf canopy was shed in 167 days (October 3, 1979 to January 17, 1980) with 86% of the leaves falling during the first 24 days. Surface area of fallen sugar maple leaves during this autumn was $3.6\text{ m}^2/\text{m}^2$ of soil surface (Dindal and Dindal, unpubl.). Also, we found the majority of the leaf litter was incorporated on site by the following April (Tardiff and Dindal, 1980); thus the potential physical and chemical properties of the previous leaf litter fall are accessible within soil by the following growing season. Such a rapid rate of input of organic compounds and fiber via leaf material is of considerable ecological significance related to soil structure and micromorphology.

Earthworms, *Lumbricus terrestris* L. (Hamilton, 1983) and isopods, *Oniscus asellus* L. were the dominant biotic mediators of incorporation of leaf litter on the New York site. The remainder of the maple leaves, not consumed by earthworms, were skeletonized by the isopods, with the removal of 91% of the leaf (mostly mesophyll and palisade tissues) leaving the 9% fibrovascular bundle leaf structure intact. The obvious increase in surface area resulting from skeletonization is phenomenal; isopods reprocess leaf tissue into numerous fecal pellets each with an average surface area of 3.3 mm^2 . Each pellet is a rectangular solid averaging 1.1 mm long with a 0.6 mm square end. In addition to the incorporation of these pellets into the soil, *Oniscus* also produces a network of $0.33\text{ m}^2/\text{m}^2$ of fibrovascular bundle "lace" destined for soil microsites. This network provides potentially active sites with capacity for cation exchange and a cellulose/lignin matrix onto which soil minerals may be further physically and chemically bound.

Carrion Deposition

Carrion, invertebrate exuviae and carcasses of vertebrates comprise important components of soil litter even though they are less obvious or deliberately ignored. Carrion falling to the soil surface deposit various elements, biochemical compounds and energy sources that support decomposer food webs. Heterotrophic microcommunities quickly colonize, use and distribute the structural ingredients of highly proteinaceous vertebrate carcasses. Nitrogenous and sulphur laden compounds seep into the adjacent soil. Molecules that are naturally recalcitrant, like chitin which contains nitrogen radicals, scleroproteins with both nitrogen and sulphur moieties, calcium and magnesium carbonate-protein complexes and even organosiliceous compounds, can originate from decay of invertebrate and vertebrate carcasses. They are buried, directly or indirectly, providing unique slow release compounds as well as extraordinary organic

matter substrates on which and from which soil fabric is produced.

Fecal Rain

Animal defecation constantly subjects the earth's surface to a "rain" of feces. These nutrient/energy-rich additions to soil sediments are extremely subtle, even more so than the fall of carrion. Perhaps the holistic effects of this omnipresent phenomenon would never be totally appreciated unless *all* organisms evacuated at exactly the same moment! Because defecation is a natural packaging, recycling process by which biochemical compounds and energy sources are pelletized, it is very important to soil formation and to dynamics of decomposer food webs. Fecal structure, chemical composition, pellet size, and rate of deposition are species specific. These characteristics represent a wide array of variables that are interjected into substrates of all ecosystems. Fecal pellets or dung balls are, therefore, energy/nutrient dissemules that are formed, transported and distributed onto the earth's soils by all kinds of animals.

SPECIFIC BIOTIC PROCESSES AT ORGANIC/INORGANIC INTERFACES

Total functions of decomposer microcommunities in association with unique microhabitats are responsible for processes such as soil fabric production, translocation, and transformation which ultimately lead to fabric reorganization and "soil ripening" as per Bal (1982). These are part of the biological activities referred to by Kubiena (1948) as the "principal driving forces of any soil forming processes." Several biologically mediated processes warrant more specific comment.

Slime and Gum Production

Mucopolysaccharides and other carbohydrate complexes are produced by many soil decomposer organisms within their soil/litter realm. Slimes and gums are exuded as metabolic byproducts, lubricants for mobility, forms of chemical and physical defense, modes of substrate attachment, and mechanisms for food-getting and pheromonal dispersal agents. In addition to their adaptive roles, these compounds may directly or indirectly cause or aid in formation of soil aggregates causing organic and abiotic materials to adhere forming erosion-stable units. In turn, this gives specific character to both the micro- and macro-structure of soil, *i.e.*, increasing organic matter incorporation, water holding capacity, porosity and ion exchange capacities. Also, the metabolism of the soil ecosystem is enhanced by the subtle monomolecular layers of slime that are potentially important microsubstrates for soil microbial colonization and population maintenance.

Coprophagy and Geophagy

Eating soil or mineral materials - *geophagy* (Jones and Hanson, 1985; Kramar, 1973), and consuming another individual's feces (either interspecifically or intraspecifically) - *coprophagy* (Hassall and Rushton, 1985; Simmons, 1983; Anderson, 1978; Kenagy and Hoyt, 1980), is not uncommon in the natural world. With future research, many more examples involving soil animals are likely to be documented. In the observed examples of coprophagy, a diversity of organic compounds, already subjected to an initial digestion are further subjected successively to the digestive processes and gut symbionts of new consumers. Inorganic and organic substances are forced together very closely within a gastrointestinal microhabitat and eventually incorporated into the soil matrix. Large fecal masses or pellets are altered

chemically; they are reduced to smaller and smaller units, increasing in surface area and thus having particular impacts on the soil micromorphological structure and function.

Insertion of Organic Matter

Both invertebrates and vertebrates exhibit habits that cause many forms of organic matter to be inserted into soil thus modifying the soil fabric. Mammal burrows filled with organic material within soil profiles were recognized as Krotovinas by early agronomists. Birds which nest in ground burrows, such as the burrowing owl (*Speotyto cunicularia*), bank and cliff swallows (*Riparia r. riparia* and *Petrochelidon pyrrhonota*) and the belted kingfisher (*Megaceryle a. alcyon*) all deposit and interject various organic compounds during production of their annual broods. Along sea coasts and above intertidal lines, crabs regularly bury carcasses and other organic debris. Dung beetles (Stevenson, 1983; Brussard, 1985), some spiders like *Geolycosa* (Shelford, 1913), ants, and enchytraeid and lumbricid worms constantly bury or intertwine organic matter with soil particles. Dipteran maggots migrate from their decayed food source, burrow and then pupate within the surrounding soil; most edaphic pupae die and decay in this buried state (Dillon, 1984; Hall, 1947).

Although each interposition of organic substance may be relatively microscopic when viewed from the macroecosystem level, the constancy of pattern, the regularity and ultimate sum of biotic input via these subtle and mundane processes greatly influences soil micromorphology and structure. Such active processes led Jenny (1980) to classify soil invertebrates functionally as "mechanical blenders" of soil. The insertion-upwelling activities are perhaps analogous to the action of the sewing machine where organic compounds are threaded into soil fabric following a specific spatial and temporal pattern; each stitch, no matter how minor, has its functional and structural role.

Upwelling of Inorganic Matter

Certain soil animals are responsible for mining and deposition of large quantities of mineral materials on soil surfaces. Burrowing rodents unearth and build surface mounds that have the heterogenous physical characteristics and textures of deeper soils. Upwelling not only influences the below-ground soil fabric but also noticeably shapes the surface landscape, whether caused by mound-building ants (Werner, 1984) or by fossorial rodents (Cox, 1984). Less noticeable, but of equal importance, are the excavations of mineral soil by non-mound building ants and earthworms. In a central New York old field, 78% of the mineral soil particles excavated by the ant, *Lasius niger neoniger* Emery, are within the 180–425 μm size range (Dindal, pers. obs.). Possible species specificity of size selection of soil particles and movement by ants is probably an important factor in soil formation. We observed species specificity of soil aggregate (fecal casting) size formation relative to several dominant earthworm species (Dindal, Theoret and Moreau, 1978); also *Lumbricus terrestris* populations are highly correlated with presence of 4.0 mm water-stable soil aggregates (Hamilton, 1983). From these studies specific size relationships of soil aggregates to their biotic source are suggested (Table 1).

Gradual Comminution

Constituents of ingested plants and animals are radically transformed into complex forms and new compounds as they pass through the guts of large and small grazers and carnivores. These materials are microbially primed and again low entropy is facilitated (this time by

Table 1: PROPOSED SIZE RELATIONSHIPS OF EROSION-STABLE SOIL AGGREGATES TO EARTHWORM SPECIES AND THEIR SYMBIONTS.

SOIL AGGREGATE SIZE (mm)	SOIL BIOTIC SOURCE OF FORMATION
> 6.4	Symbiotic complex of earthworms, roots and microorganisms
4.0	<i>Lumbricus terrestris</i> L.
2.0	<i>Aporrectodea tuberculata</i> (Eisen)
1.0	<i>Octolasion tyrtaeum</i> (Savigny)
0.5	<i>Lumbricus rubellus</i> Hoffmeister
0.5	<i>Dendrobaena octaedra</i> (Savigny)
0.25	<i>Dendrodrilus rubidus</i> (Savigny)
0.15	Microorganisms

symbiotic relationships) as the food bolus is gradually transposed into feces.

Expelled remnants of ingesta that are packaged in dung pellets provide two surface area configurations different from the original form of the food. The initial size and surface area of the fecal pellet are functions of the rectal and cloacal organs and the anal cross-section. Species specific pellet size determines potential interspecific coprophagic efficiency and provides a unique microbial substrate within the soil microecosystem. As the pellet breaks down, a second potential surface area increases dramatically as dung constituents are exposed. These materials are the function of mastication, peristalsis and digestive activities and represent the maximum size reduction of food eaten by a given consumer. These secondary particles, which are finely divided, blend with the surrounding mineral particles and thus reflect the specificity of the animal species on soil formation.

For example, the surface area of the fragments of herbaceous fabric comprising fecal pellets of the cottontail rabbit, *Sylvilagus floridanus*, in central New York is 10 times greater than the surface of the individual entire ovoid pellet (Figure 1). Such a modification in the vegetation of the secondary fecal fragments deposited on or in the soil greatly increases the potential for organic/inorganic interfaces. Microbial and decomposer invertebrate activity, which is vitally important in the genesis of soil micromorphology, is stimulated.

SUMMARY

Understanding soil fabric production demands a holistic, cybernetic approach; this includes a multivariate consideration of all physical, chemical and biological intricacies of the soil, both macroscopic and microscopic, within ecological spheres of influence. The rhizosphere was one of the first of these ecological spheres of influence to be recognized, illustrating the microhabitat/microcommunity dynamics related to plant root systems. Phyllospheres have been conceptualized to study aerial microhabitats and microcommunities on surfaces of living leaves (Preece and Dickinson, 1971). We described the vermisphere (Hamilton and Dindal, 1983), another ecological sphere of influence within soil, which shows delicate biotic/abiotic

POTENTIAL SURFACE AREA of COTTONTAIL RABBIT (*Sylvilagus floridanus*) FECAL PELLETS

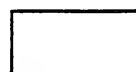
MAY 1984

ENTIRE ($n=4$)

SURFACE AREA
($\bar{x} \pm SE$)



$2.1 \pm 0.2 \text{ cm}^2$



DISSECTED PELLETS

HERBACEOUS FABRIC

$25.6 \pm 0.5 \text{ cm}^2$

KENTUCKY BLUEGRASS

ORCHARD GRASS

DANDELION

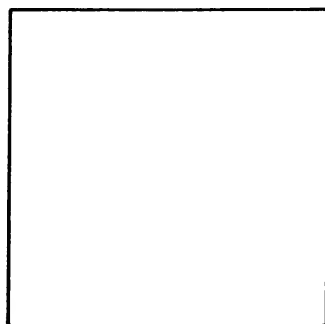


Figure 1.

interactions associated with earthworm burrows. Based upon unique soil microcommunities and related microhabitats emphasized in this paper, I propose the following additional microecosystem concepts to aid in research, communication and understanding of animal involvement in soil fabric production:

1. Edaphophyllosphere (=edaphic phyllosphere) - sphere of influence of the fallen leaf and vegetative litter as a soil microhabitat,
2. Coprosphere - sphere of influence of vertebrate and invertebrate fecal material as a soil microhabitat,
3. Necrosphere - sphere of influence of vertebrate and invertebrate carcasses as soil microhabitats,
4. Nidusphere - sphere of influence of vertebrate and invertebrate nests, nest sites and burrows as soil microhabitats.

The active result of the structure and function of the specific microcommunities inhabiting each of these microecosystems governs the immediate soil fabric formation and plays an ultimate influential role in the characteristic genesis and maintenance of any given soil.

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FAUNAL INFLUENCE ON SOIL MICROFABRICS AND OTHER SOIL PROPERTIES

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ABSTRACT

The influence of animal activity becomes visible by studying thin sections of soil with microscopes. Several specific soil microfabrics (organic laminae, lenticular fabric, lamellar fabric, mesh fabric, cross hatching) that are directly associated with animal activity are recognized. However, more research is needed to understand the role of the fauna and specific animals in the formation of soil fabrics. A restricted number of other micromorphological features (fecal pellets, inorganic pellets, faunal tubules and chambers and mammilated metavughs) identified so far are used only to indicate the presence of faunal activity in soils. Animals may significantly alter the soil characteristics and have an important role in the chemical decomposition of plant residues and the accumulation of nutrients in the biomass. Their excrement, together with organic residues, is essential in the formation of soil aggregates. Faunalurbation facilitates deep rooting, and consequently, higher production of biomass.

RÉSUMÉ

L'influence de l'activité des animaux devient apparente lorsqu'on étudie au microscope des coupes fines du sol. L'auteur reconnaît plusieurs microstructures spécifiques du sol qui sont directement associées avec des activités animales (feuilletés organiques, structure lenticulaire, structure lamellaire, structure en maille, double hachure). Toutefois, plus de recherches seront nécessaires pour comprendre le rôle de la faune dans son ensemble et celui d'animaux spécifiques dans la formation des diverses structures des sols. Un nombre limité d'autres traits micromorphologiques qui ont été identifiés (boulettes fécales, boulettes inorganiques, petites galeries et chambres d'animaux, et métavughs mamelonnés) ne sont pour l'instant utilisés que pour indiquer la présence d'activité animale dans les sols. Les animaux peuvent altérer d'une manière significative les caractéristiques des sols et jouent un rôle important dans la décomposition chimique des résidus végétaux et dans l'accumulation des éléments nutritifs dans la biomasse. Leurs excréments, combinés avec les résidus organiques, sont essentiels à la formation des agrégats des sols. Le remuement causé par la faune facilite l'enracinement en profondeur et, par conséquent, favorise la production d'une biomasse plus élevée.

INTRODUCTION

Every soil provides a habitat suitable for animal life. Because of the presence of large quantities of living and dead plant and microbial materials which serve as a continuous food resource, soil animals are generally restricted to the organic or mineral surface horizons. However, animals may also be active at lower depths.

In his early studies, Kubiens (1938) pointed out that the association, activity and structure of soil organisms are primarily controlled by the space condition, microclimate (temperature, moisture, air pressure, insolation, and air movement), pH and salt concentrations, and food conditions in the microhabitat. The heterogeneous nature of soil provides a variety of habitats in which animals can survive and reproduce.

Aquatic forms such as protozoa and nematodes restrict their lives to the moist zone where free or capillary water is available. Apart from these aquatic forms, soil animals are organized into two major groups as suggested by Lee and Wood (1971): (i) animals unable to burrow, and (ii) animals that burrow and reshape the soil. Because of the changes taking place in the soil year-round such as heating, desiccation, freezing of the surface and/or sheltering from predation, members of the second group have the ability to accommodate themselves quickly by moving to a soil zone that meets their requirements. Despite the concentration of biological activity in surface horizons (Bal, 1970; Whittaker, 1974; Bal, 1982), tracks of small soil animals were found down to 150 cm, even in soils of arctic and subarctic regions (Federova and Yarilova, 1972). In semi-arid climatic regions, many animals commonly occur down to 3 m (Kubiena, 1953; Price and Benham, 1977; Valiakhmedov, 1977a,b).

Improvement in preparation techniques for thin sections of soil has made it possible to directly observe and study the influence of biological activity and the role of animals in soil genesis. Much of our present knowledge results from the pioneering studies and efforts of Zachariae (1965, 1967) who described the development of humus forms by specific soil fauna. Attempts were also made, especially in semi-arid and arid regions, to establish the relationship between particular groups of animals and the soil types (Valiakhmedov, 1977a, b; Ghilarov, 1978). Because of the complexities in temperate humid regions, Bal (1982) found great difficulties in the interpretation of the relationship between the soil and its community. The major problem today is the lack of study in the interface between biology and pedology.

Several signs of animal activities are found in thin sections of soil. Excrements are one of the easily recognized features which characterize the nature and the feeding habits of the animals. Structures within the soil body such as chambers, including pupal chambers of soil dwelling invertebrates described by Valiakhmedov (1977a, b) and pedotubules described by Brewer (1976) are other important features that may be used in recognizing and understanding animal activity in soil. As well, studies indicated that a certain part, or even an entire profile, can be partly to completely reworked by animal activities (Buntley and Papendick, 1960; Mulders, 1969; de Meester, 1970; Valiakhmedov, 1977a, b; Bal, 1982). Such mixing processes are referred to as "faunal pedoturbation" (Hole, 1961; Jongerius, 1970).

Despite the efforts made in the past, our present understanding of soil animals and their effects on soil characteristics seems to be far from complete. This paper is aimed only at elaborating on the present level of knowledge on micromorphological features that are formed by animal activity. As an integral part of the interpretation of soil micromorphology, faunal effects on other soil properties are also included in the present report.

FAUNAL INFLUENCE ON SOIL FABRIC

A wide range of soil microfabrics are directly associated with animal activity in soils. However, at this stage there is a need for detailed micromorphological studies to fully understand and recognize the special soil fabrics which are induced by the faunal activities. As an attempt in this direction, the information noted below was summarized from a few available studies dealing with the microstructure of termite mounds (Stoops, 1964; Lee and Wood, 1971, Sleeman and Brewer, 1972 and Mermut *et al.*, 1984). Microfabrics so far recognized in termite mounds (landscape features that are entirely biologically produced) include organic laminae, lenticular fabric, lamellar fabric, cross hatching and mesh fabric, which are considered to reflect the process of construction of the termite nest, and comprise remnants of their activities

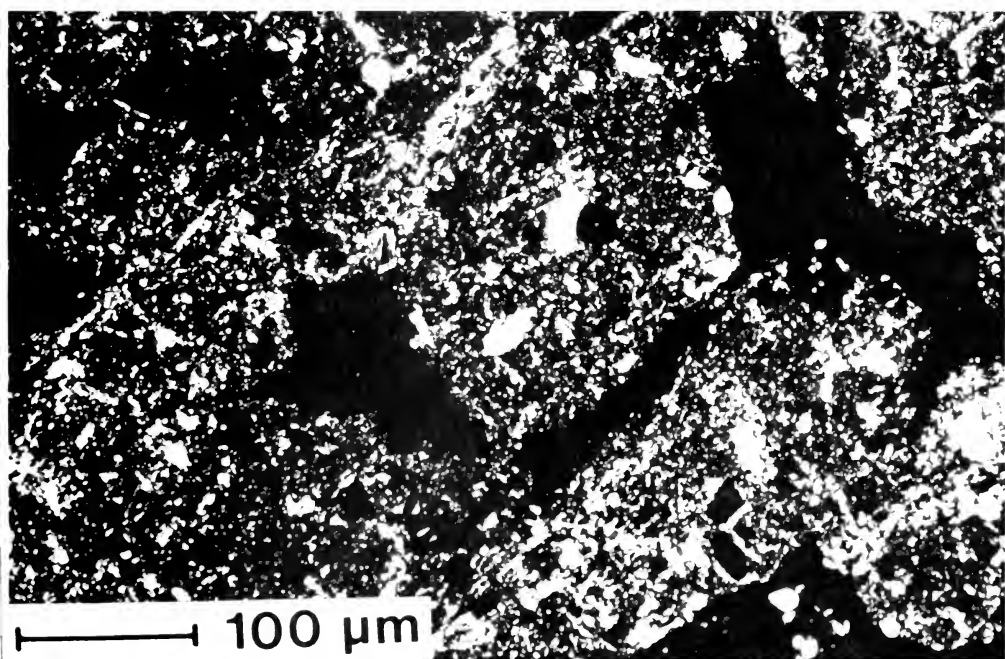
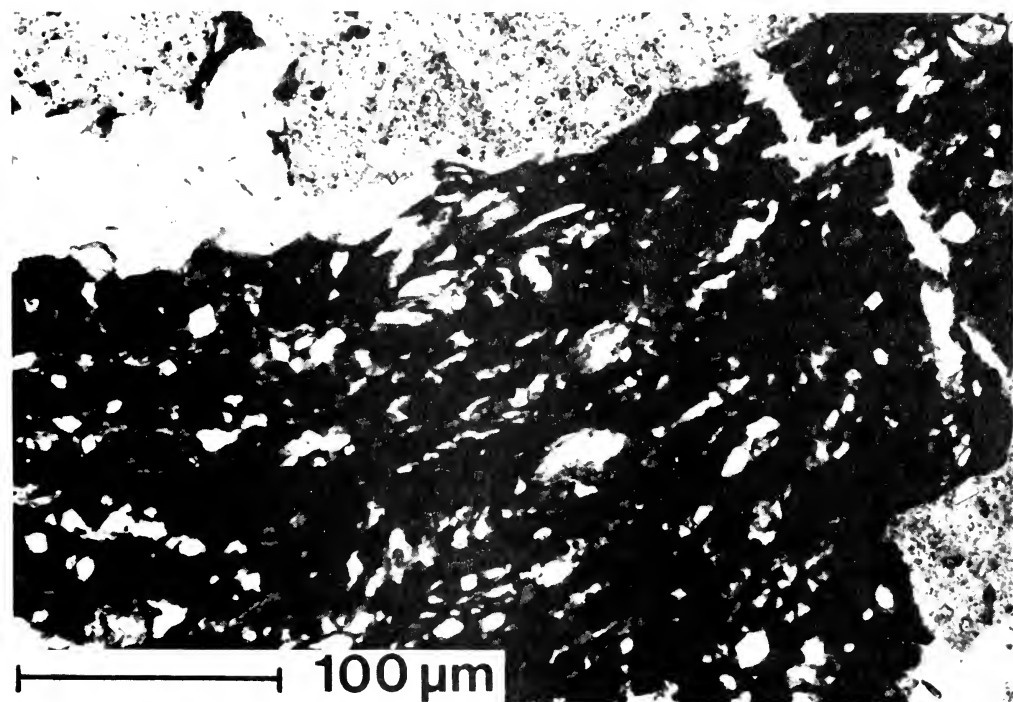


Fig. 1. Organic laminae (dark areas) and lenticular-fabric. *Macrotermes subhyalinus* gallery wall from Kenya (plane light). Fig. 2. Lenticular fabric formed by lenticular units. *Macrotermes subhyalinus* nursery section from Kenya (crossed nicols).

in the soil.

Organic Laminae

These consist of dark reddish brown to black, very weakly and strongly anisotropic material occurring as bands commonly 20 μm wide found adjacent to existing gallery walls (Fig. 1) or within gallery fills. Their distinctive color allows an easy recognition and delineation of boundaries with the microscope. Organic laminae may be characteristic for certain termite species. They are richer in organic matter than the surrounding soil material. According to Lee and Wood (1971), they are likely made of excrements with a semiliquid consistency. Organic matter in some of the laminae is more highly humified than in others. More melanization, considered as an indication of increased humification, suggests that this organic material has passed through the gut of the termite.

Lenticular Fabric

The elongated lens-shaped units found in termite mounds were described as lenticular by Stoops (1964). Strong welding of single small lenticular units may develop into a large lenticular unit exceeding 5 mm in size (Mermut *et al.*, 1984). Low content of skeleton grains and high amount of inorganic plasma encourages the formation of larger pellets (Fig. 2). The units consist of dominantly mineral plasma and some pedological features, skeleton grains and little organic matter. Micromorphological observations indicate that each unit consists of different proportions of plasma and skeleton grains. The fabric consists of strongly accommodated lenticular units.

Lamellar Fabric

Fabric consisting of alternate parallel alignments of skeleton grains and plasma in which the parallel arrangement is sometimes associated with planar voids was termed "lamellar structure" by Stoops (1964) and "lamellar fabric" by Sleeman and Brewer (1972). This fabric was found in soils which had high contents of both sand and silt. The skeleton grains are embedded within the soil matrix; the plasma shows extremely well-developed masepic fabric. Because of the parallel arrangement of clay domains, Stoops (1964) termed this fluidal structure. The groundmass of such structures appears to be very dense. Aside from the above-mentioned planar voids, there are no voids visible in such a fabric. The majority of the colors of the groundmass in the lamellar fabrics are similar to the original soil plasma from which the mound was built. However, addition of humic particles may cause the plasma to be somewhat darker in color.

Cross Hatching

This may be considered a subtype of lamellar fabric in which two sets of parallel arrangement of plasma and skeleton grains cross each other (sometimes 90°). The resulting feature is like lattisepic fabric of Brewer (1976), which by definition considered only the arrangement of the clay domains. This type of fabric is found near the gallery surfaces of termite mounds (Mermut *et al.*, 1984) (Fig. 3). Our experience so far indicates that both lamellar and cross-hatching can be considered to result from activity of burrowing animals.

Mesh Fabric

This fabric type results from the specific arrangement of either spheroidal or lenticular construction units. Each construction unit has a separation zone of plasma that can be compared with skelsepic fabric (Brewer, 1976). Welding of individual units in a preferred direction results in a type of plasma orientation resembling a mesh, called "mesh fabric" by Mermut *et al.* (1984). If strong welding occurs in each construction layer, the borders of earlier units appear more diffuse. This type of fabric is attributed to the homogeneity as well as high content of plasma.

OTHER MICROMORPHOLOGICAL FEATURES FORMED BY ANIMAL ACTIVITY

This group includes fecal pellets, pellets built as construction units, faunal tubules and chambers, and mammilated metavughs.

Fecal Pellets

Fecal pellets are the excreta that have left an animal's intestines as shaped, three-dimensional units (Bal, 1973). Recognizable fecal pellets can be seen in a pedotubule, inorganic horizons (Fig. 4), or within large interconnected pore spaces. Unfortunately, little is known about the morphological characteristics of the fecal pellets. Brewer (1976) suggested that a major subdivision of fecal pellets can be based on the external shape. Bal (1973) was able to distinguish five main groups: spherical (Fig. 5), ellipsoidal, cylindrical, platy and threadlike. Bal suggested that one should study and describe the characteristics in the following order of succession: shape, size, composition, basic distribution.

Easily recognizable fecal pellets are found in burrows (Fig. 6), tunnels or chambers, which may extend deep into the profile. Therefore, this feature subjected to the proper recognition can be used as an absolute indication of biological activity. However, as a result of a disturbance of soil material, for example by pedoturbation, the fecal pellets may become embedded in the soil material, and thus become difficult to identify and describe.

Pellets Built as Construction Units

Pellets built as construction units are termed "construction elements" by Stoops (1964). Those units recognized in termite mounds are composed of skeleton grains, plasma, and pedological features. They are spheroidal, ovoid or lens-shaped and vary in size from 125 μm to 1000 μm . Mermut *et al.* (1984) described two distinct types of pellets; one is highly isotropic, light yellowish in color with more clay mineral plasma appearing to be oral pellets mixed with saliva, and the other is brownish, slightly isotropic probably mineral plasma mixed with excreta. According to Arshad (1981), some *Macrotermes* species selectively prefer fine soil separates (particles less than 0.5 mm) to construct their mounds. Lee and Wood (1971) indicated that in a Podzolic soil, the termites preferred to use clay-rich subsoil to encase their mound. Stoops (1964) observed that, during restoration of a mound, the termites piled up the little units of sand and clay, moistened with their saliva. Quick-drying of the outer crust of the pellets creates a plasma separation around each unit, allowing their recognition, even when they are extremely welded. This separation of plasma is comparable to the skelsepic plasma fabric of Brewer (1976). Except for granular aggregates found in the cracks of the Vertisols which resemble these units, pellets can also be used as a sign of biological activity in non-self-mulching soils. However, the random distribution pattern of the granular aggregates in the swelling clay

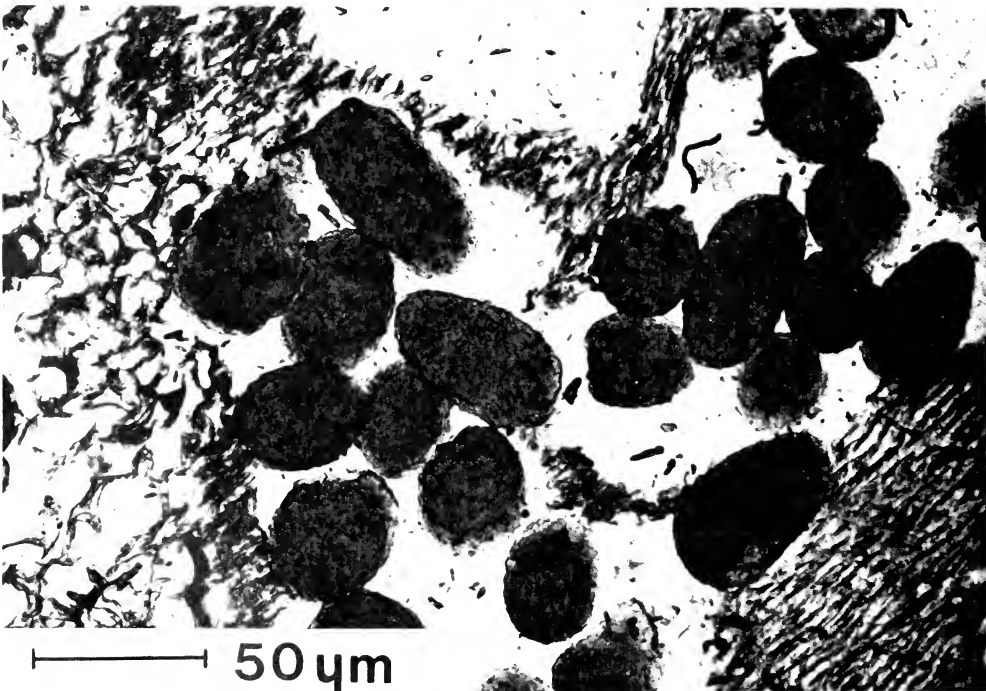
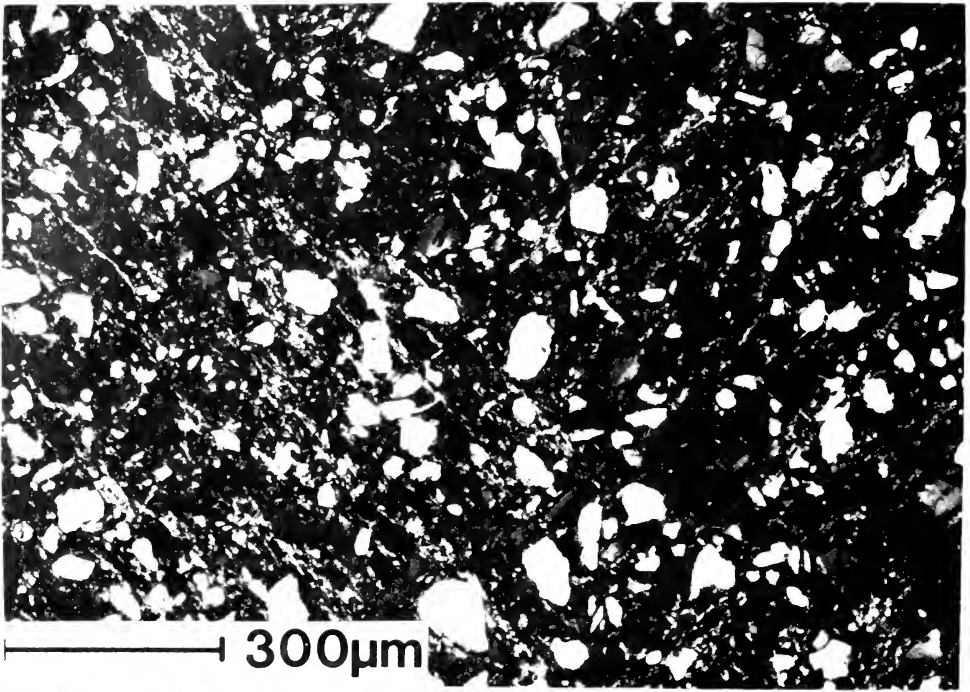


Fig. 3. Cross-hatching observed in a *Macrotermes herus* mound from Kenya (cross nicols). Fig. 4. Single organic ellipsoidal fecal pellets from the organic horizon of a Luvisolic forest soil in Saskatchewan (plane light).

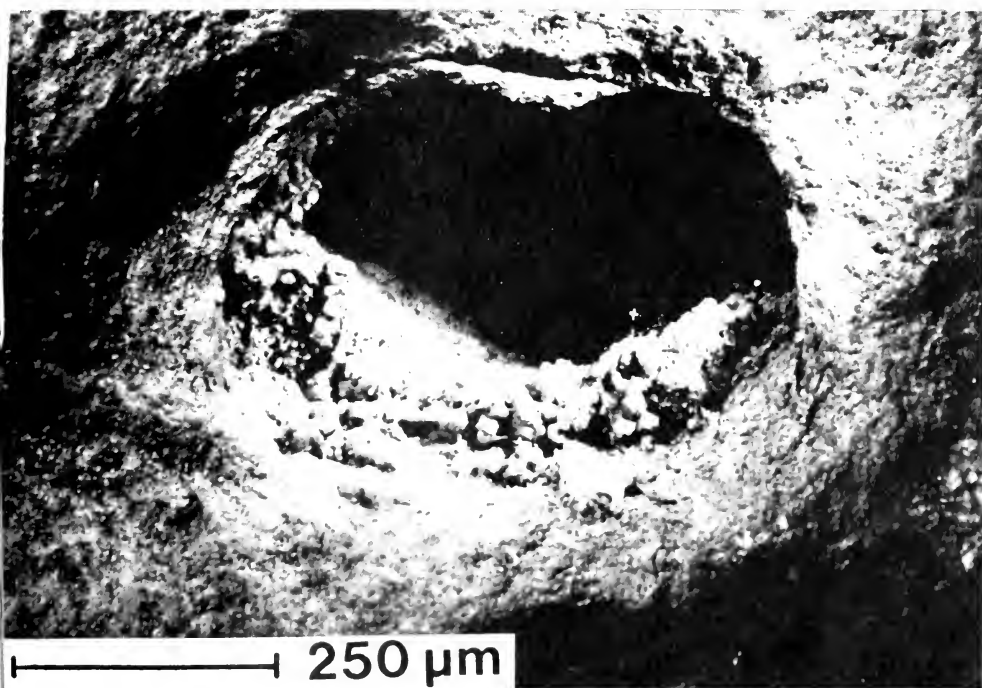
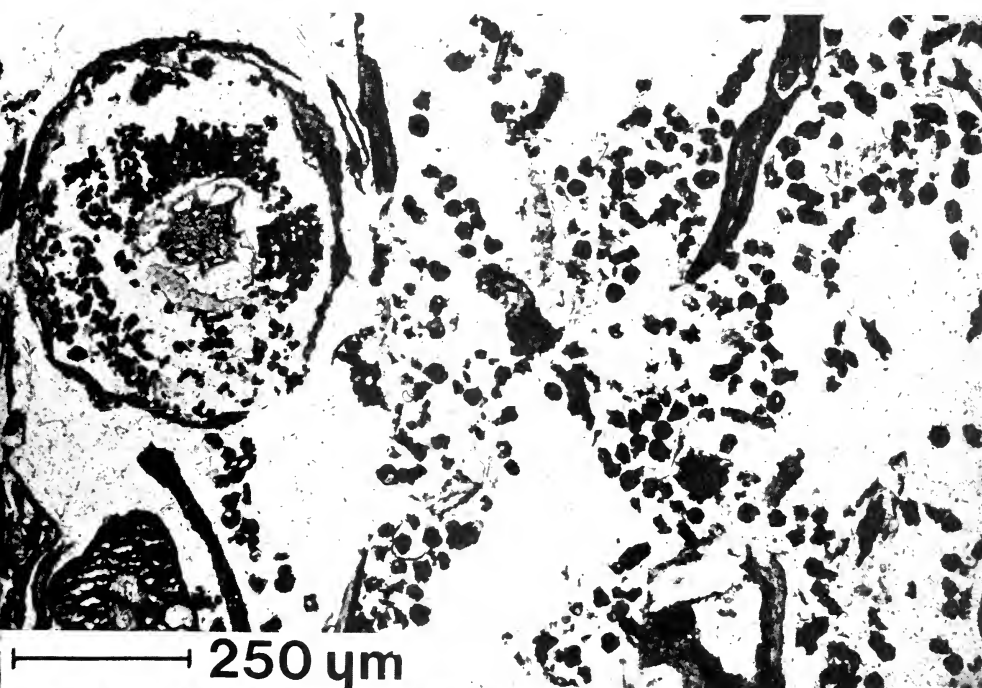


Fig. 5. Single organic spherical melanized fecal pellets from the organic horizon of a Luvisolic forest soil in Saskatchewan (plane light). Fig. 6. Fecal pellets around a zoogenic tube (an African termite burrow), as seen with a binocular microscope.

soils may serve to differentiate the pellets even in these soils.

Faunal Tubules and Chambers

These are features which have sharp external boundaries and are generally larger than the voids in the soils. Faunal tubules have a tubular external form and are made by soil animals that can burrow and reshape the soil materials. Tubular-shaped voids can also be formed by growing roots and may be confused with faunal tubules. Characteristics like wall lining (Bal, 1973) and imprints caused by the bodies of animals may be used to identify zoogenic tubes (Jongerijs and Reijmerink, 1963). Excreta in tubules support their origin as faunal burrows.

The burrowing of earthworms is more uniform and generally larger than the tubular-shaped voids produced by growing roots. The voids created by earthworms are the same diameter as their body. However, it is not always possible to use size of the burrow to identify the animals responsible for construction of tubules in the soil. For example, termites and ants make a tubule much larger (Fig. 6) than their bodies; however, we know now that these animals produce special soil fabrics around their burrows.

Chambers differ from large voids in soils in that their walls are regular and smoothed (Fig. 7). Their formation has been attributed to faunal activity. In termite nests, chambers have arched or domed roofs and relatively flat floors. As can be clearly seen in Fig. 6, animals (for example, termites) sometimes coat the walls of their tunnels with clay, forming a smooth cutanic feature. Dark staining of gallery walls which is a characteristic found in termite mounds can also be attributable to faunal activity. Surface smoothing, discoloration of burrows, cementing and dense packing and excreta in voids are other characteristics that can be recognized in soil thin sections.

Mammilated Metavughs

As indicated by Brewer (1976), these special vughs have smoothed walls and mammilated conformation. Mermut *et al.* (1984) found this special void in almost all the thin sections from the African termite mounds. Brewer (1976) reports that mammilated vughs occur commonly in soils with strong evidence of extensive faunal activity, especially earthworms. The voids are formed by either welding of pellets used for mound construction (Fig. 8) or faunal excreta. Coalescing fecal pellets and/or pellets used for construction may form empty spaces with sharp protuberances. For pellets used for construction, the plasma reorientation around each unit is clearly observed. Therefore, the soil matrix in contact with the vughs invariably shows a vosepic plasmic fabric. Mammilated metavughs often bear some additional marks (orderly arrangement of units, darkening of soil material with increased density) which can be used for further evaluations. Many mammilated vughs may serve as good indicators of animal activity in soils.

FABRICS FORMED BY DECOMPOSITION OF ORGANIC MATTER

Soil animals play a very important role in fragmentation of litter and redistribution of organic materials in soil. Excrements of different shape, size, color, orientation, and composition indicate consumption of litter by soil fauna. Some of the animal species, as for example enchytraeids (Zachariae 1964) consume decaying arthropod faeces, pierce and cleave the compact excrement of big earthworms, and eat humus earth as well. Thus, decomposition is a continuous process in which the animals work in close association. All plant residues and

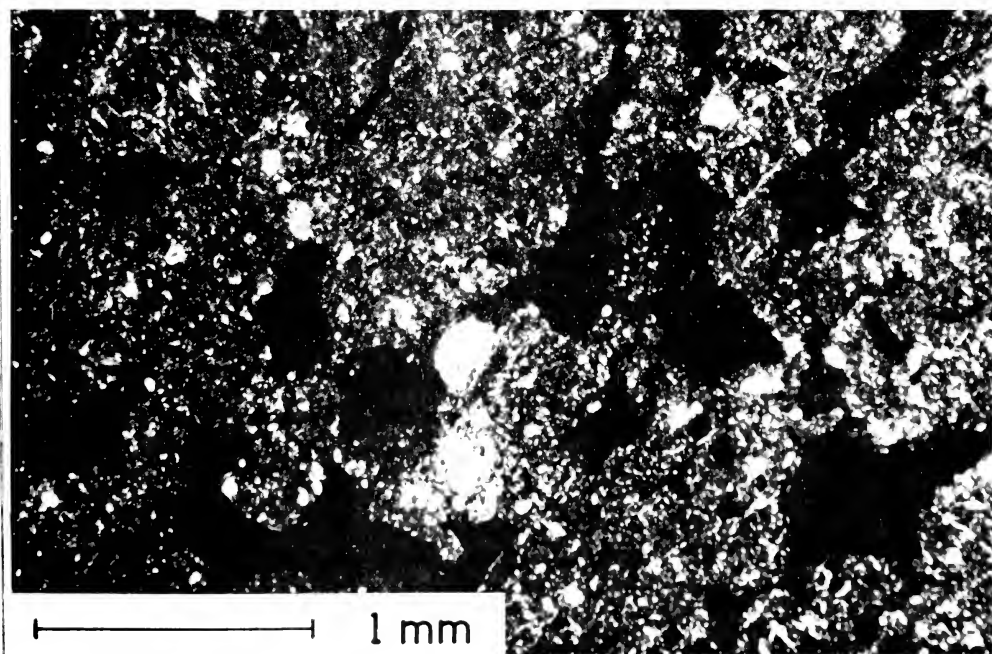
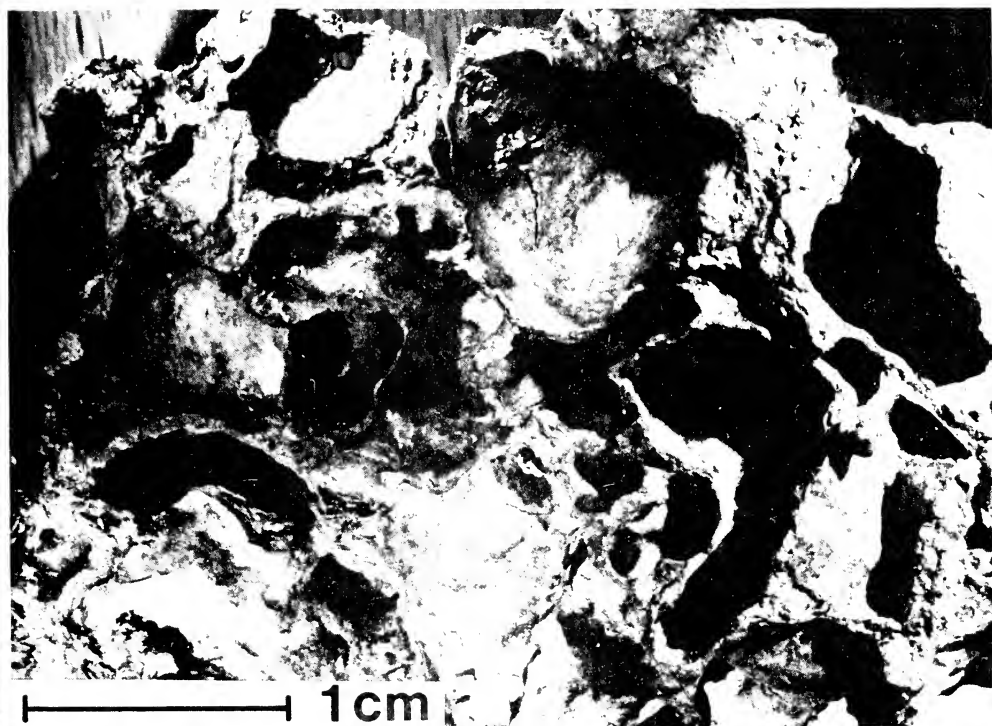


Fig. 7. Interconnected chambers built by an African termite species, as seen with a binocular microscope. Fig. 8. Mammilated metavughs formed by coalescing of organic pellets used for construction from an African termite mound (crossed nicols).

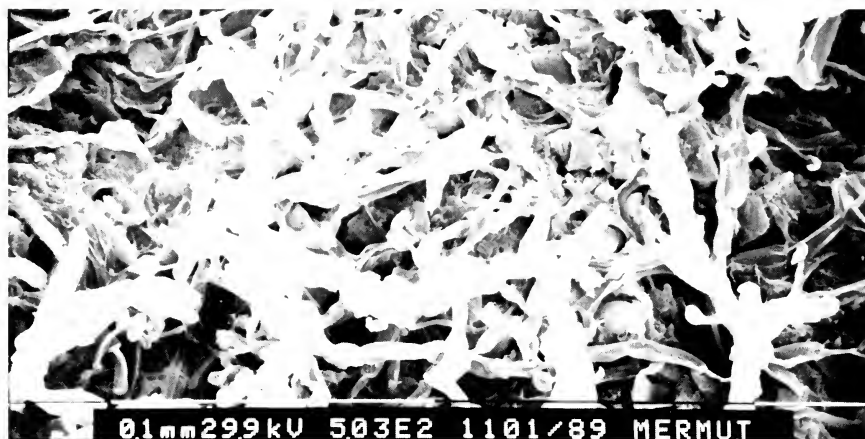


Fig. 9. SEM micrograph of a comb from the nest of an African termite (*Macrotermes michaelseni*). The comb appears to be constructed from plant fragments.

especially excrements are also subject to further microbial decomposition. The effect of specific soil animals on soil microflora (Arshad *et al.*, 1982) is becoming an important area for investigation. Fecal pellets are found with fungal hyphae, indicating their close association during decomposition of organic matter.

According to Geyger (1967), excrement together with organic residues are essential in the formation of soil structure, especially in organic horizons depending on the decomposition stage of organic matter and the admixture of inorganic plasma and skeleton grains. Brewer and Pawluk (1975) have recognized certain types of granic and related fabrics, especially in the organic horizons of some Canadian soils. Their concept is strictly based on morphology; however, it can be related to soil genesis. It seems quite clear that more research is needed to understand the role of the fauna in the formation of soil fabrics.

Soil animals in organic horizons have a role in chemical decomposition and humification of plant residues and therefore accumulate nutrients in the biomass. Babel (1978) demonstrated that rate of fabric differentiation increased from the L to F and decreased in the H horizons, indicating the close positive relationship between humification and population of soil fauna. Despite research efforts in this area, details of these processes are still unknown.

In tropical countries, termites are capable of decomposing up to a third of the fresh annual grass, wood and leaf litter (Collins, 1981). This makes them the most important group of invertebrates in the decomposition of organic matter in their natural habitat. It is interesting to note that the fungi of the genus *Termitomyces* are the predominant microorganisms growing on the comb in certain termite nests. As can also be seen in Fig. 9, the comb is made up of mostly uningested plant materials (Rohrmann, 1978) and/or termite fecal pellets (Sand, 1960). Fungus cultivated on the comb was of nutritional value for the termites. This indicates a well-balanced cycle of organic matter in a harmony in which the termites have an important role.

INFLUENCE ON OTHER SOIL PROPERTIES

About 1.5 million kinds of animals are living on more than a million kinds (equivalent to the soil series, U.S. classification) of soils (Buol, *et al.* 1980). The action of soil fauna in combination with plants on initial parent material is prerequisite to soil formation.

Turbation of soils by animal activity (faunal pedoturbation) is generally well known to the pedologist (e.g., Hoeksema, 1953; Slager, 1966). Krotovinas (Soil Survey Staff, 1951) are common features of Chernozem and dark colored soils commonly developed under prairie vegetation. They are the result of infillings of animal burrows by transportation of soil material from any direction. This contributes to the process of soil homogenization. Krotovinas appear in various sizes and are texturally and structurally unlike the surrounding soil materials. In semi-arid soils of Turkey, de Meester (1970) found that the contents of organic matter and nitrogen of krotovinas and the root development in krotovinas were considerably higher than the soil material of the horizon in which they existed.

Worm-worked soils are typical examples of how an animal group may significantly alter the soil characteristics. Such unique soil profiles were reported in several places in North America (e.g., Buntley and Papendick, 1960; Nielsen and Hole, 1964; Wilde, 1971). Striking differences in macromorphological features and certain chemical characteristics are evident between the worm-worked profiles and the non-affected adjacent areas. Horizon boundaries within theurbation zone were obliterated. Buntley and Papendick (1960) clearly demonstrated that the B horizon which had high clay content originally was reduced in clay with the materials transported from both A and C horizons. As a result, the clay content of the A and C horizons were increased, whereas the B horizon was decreased. There was a distinct increase in organic matter and nitrogen content in the soils perforated with earthworms. Micropedological studies showed argillams of argillic horizons intensely reworked by faunal activities (Jongerijs, 1962). We have observed similar effects in thin sections of some Kenyan Oxisols perforated by termites. Preferential selection of clay for mound construction by some termite species (Stoops, 1964; Lee and Wood, 1971) can cause a complete mixing of all horizons in Podzolic soils and soils with higher clay content in the subsoil than the topsoil.

It has long been recognized that the biological homogenization of soils is also of great importance in land reclamation from the sea sediments (Hoeksema, 1953; Slager, 1966). In the sediments of the famous IJsselmeer polder, Bal (1982) observed that many channels which were formed by animals facilitated the deep rooting and consequently higher production of biomass.

Based on apparent lack of the original soil characteristics in worm-worked soils in South Dakota, Buntley and Papendick (1960) suggested that such soil be named "Vermisol". These soils display the features resulting from intensive perforation of worms. The humus type of forest soil mixed by earthworms is called a "Vermiol" (earthworm mull) by Wilde (1971). The recognition of such soils resulted in the establishment of the three great groups, namely, Vermiborolls, Vermudolls and Vermustolls in the Soil Taxonomy (Soil Survey Staff, 1975). These soils have a mollic epipedon that, below any Ap horizon, has 50% or more by volume of wormholes, wormcasts, krotovinas, or filled animal burrows of especially earthworms and their predators.

Because of the close relationship with soil organic matter, animals may play an important role in the reduction of water erosion. They create high water infiltration capacity as well as absorption due to production of organo-mineral complexes. In a detailed study, Arshad (1982) found that the soils influenced by termites were high in nutrients. This, together with favorable water availability and good drainage, resulted in a considerable increase in biomass in dry tropical parts of Kenya.

One has to be very careful in sampling, measuring and evaluating the effects of soil animals on soil properties. Micromorphometric measurements on samples reworked by animal activities (Mermut *et al.*, 1984) showed that in some parts of the biologically disturbed areas, porosity

increased; however, compaction caused a considerable decrease in porosity in other parts. Apparently, improper sampling is one of the causes of controversy among scientists on the pattern of animal activity.

Among other influences, there is an increase of the availability of mineral nutrients and their distribution within the rooting zone. For example, earthworms increased the availability of N, Ca, Mg, K, P, and Mo (Nye, 1955) and Pb, Zn and Ca (Ireland, 1975).

CONCLUSIONS

Advances in soil micromorphology have made it possible to directly observe and study the influence of soil animals on soil characteristics and the role of the animals in soil genesis. Despite the studies and efforts of the past, our understanding of soil animals and their influence on soil microstructure is far from complete. There is need for more detailed studies dealing with micromorphological features and fabrics that are associated with special soil animals.

Soil fauna together with soil microorganisms have a very important role in accumulation, decomposition and redistribution of organic matter in the soil. Some animals in the tropics are capable of decomposing up to a third of the fresh annual grass, wood and leaf litter. Because of the close relationship with soil organic matter, animals may play an important role in increasing the aggregate stability and in reducing water erosion. They increase the availability of mineral nutrients within the rooting zone and they play an important role in land reclamation from sea sediments by homogenization.

Much knowledge on the effect of soil fauna on soil characteristics can be gained by experimental studies. Breakdown of litter, formation of biopores, perforation and behavior of each animal species can be determined in cultures under controlled laboratory conditions. With the help of micromorphological studies, details of the features produced by animals can be characterized. It is certain that without such experimental studies, present problems in micromorphological identification, quantification and description of faunal activity in soils will remain unsolved.

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IN SITU LOCALIZATION OF ORGANIC MATTER IN SOILS

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ABSTRACT

Three main size classes of organic matter in soils are ingested by soil animals: (1), multicellular plant and animal remnants (5000 - 50 μm in diameter); (2), microorganisms (50 - 0.3 μm); and (3), subcellular fragments (1 μm - 10 nm). Ultracytological techniques locate particular reactive sites (polyphenolic, acidic and neutral carbohydrates, enzymes) on soil organics in situ in natural soil fabrics. This allows investigation of morphological and biochemical characteristics of organic resources available to soil animals and changes involved in organic matter transformations as materials pass from class 1 to class 3. This involves both breakdown of cellular materials and biosynthesis of new organics by microorganisms. In particular, I address such questions as: where in soils are the different size and biochemical types of organic matter located with respect to soil minerals and soil microorganisms; how are plant and animal tissues reduced to deposits of submicron and even macromolecular sizes; how do biodegradable materials (e.g., polysaccharides) escape microbial degradation; how do the physically and chemically protected organic matter deposits differ in structure, biochemistry and location; how do microbial products bind soil components into stable aggregates and how do these subsequently break down; how do these changes affect their availability and nutrient status for soil animals?

RÉSUMÉ

Il existe dans les sols trois catégories principales de grosseurs de particules organiques qui sont ingérées par les animaux endogés: 1) des restes d'animaux et de plantes multicellulaires d'un diamètre variant de > 5000 à $50 \mu\text{m}$, 2) des microorganismes d'une taille variant de > 50 à $0.3 \mu\text{m}$, et 3) des fragments subcellulaires variant de $1 \mu\text{m}$ à $10 \mu\text{m}$. Des techniques d'ultracytologie ont été utilisées pour localiser des sites réactifs particuliers (hydrates de carbone polyphénoliques, acides et netures, enzymes) sur des particules organiques en place dans les structures naturelles de sols. Cette approche permet d'étudier les caractéristiques morphologiques et biochimiques des ressources organiques disponibles pour les animaux endogés, de même que les changements qui se produisent durant la transformation des matières organiques alors que les matériaux passent de la catégorie 1 à la catégorie 3. Cette transformation comprend la décomposition des matériaux cellulaires et la biosynthèse de nouvelles substances organiques par les microorganismes. Plus particulièrement, je pose les questions suivantes: où dans les sols se situent les différentes grosseurs et les différents types biochimiques de matière organique par rapport aux minéraux et aux microorganismes? Comment les tissus animaux et végétaux sont-ils décomposés en des dépôts de taille submicroscopique ou même macromoléculaire? Comment des substances biodégradables (comme les polysaccharides) échappent-elles à la dégradation microbienne? Comment des dépôts de matière organique protégés physiquement et chimiquement différent-ils dans leur morphologie, leur biochimie et leur position? Comment les produits résultant de l'action microbienne lient-ils les composantes du sol en des agrégats stables, et comment ceux-ci sont-ils par la suite décomposés? Comment ces changements affectent-ils leur disponibilité et leur qualité nutritive pour la faune du sol?

INTRODUCTION

Little is known about organic matter in its native state in natural soil fabrics. Nearly all information on soil organics comes from studies of materials which have been chemically or physically extracted from the soil and introduced into a quite different biophysical and biochemical milieu for characterisation and quantification. Detailed knowledge of the structure, biochemistry, microbiology and location of organic materials *in situ* in soil fabrics is of great importance to determine where the various phases of organic matter mineralization occur and where nutrients are available to soil animals.

Ultrastructural studies of soil organics are concerned with particles from c.100 μm to 10 nm, so in investigations of the processes of organic matter decay and nutrient recycling, ultrastructural studies bridge the gap between materials studied by the soil micromorphologist and those studied by the soil biochemist.

Organic materials in soils are infinitely variable in their structure and biochemistry, depending on their source and the amount of microbial decay and chemical weathering they have undergone. They range in size and ultrastructural complexity from histons of plant and animal tissues which are structurally almost unchanged from their living condition down to fragments of almost macromolecular size which have undergone profound morphological and biochemical transformations (Foster and Martin, 1981).

Although modern SEMs will take specimens weighing up to 1 kg, at useful magnifications (say 10,000x) the amount of material represented in individual electron micrographs is ($<10^{-6}\text{cc}$ [see below]) so that ultrastructural studies are limited to the finer details of effects of soil animals on soil structure. Similarly the animals observed in electron micrographs of even moderate magnifications must be restricted to microorganisms - ciliates, flagellates, amoebae *etc.* Although these are very numerous in soils ($10^6/\text{cc}$ Darbyshire and Greaves, 1967), their effects on soil organic processes were until recently, much neglected. In this paper I examine the physical and biochemical environments near, and the location and structure of organic materials available to soil animals, over a wide range of sizes.

METHODS

Electron optical methods

The study of soils by electron optical methods includes the use of conventional- (CTEM) and scanning-transmission electron microscopy (STEM), scanning electron microscopy (SEM) using either secondary electron, or back scattered electron detection (BSEI), and electron probe microanalysis (EPMA) using energy (EDXRA) or wavelength (WDXPA) dispersive X-ray analysis, (Bisdom, 1983). Unfortunately, biological materials in soils consist of exotic molecular species made up of a rather limited number of kinds of atom so elemental analysis by EPMA is not widely applicable to biological problems (Hayes, 1980). Conventional EPMA instruments do not easily detect light elements such as C, N, and H, of which most organics of biological importance are composed. EPMA has been used however to investigate the distribution of P, K, Ca and Mg in roots and rhizospheres (Tan and Nopamornbodi, 1981). This review is confined to TEM and SEM studies of soil organics *in situ* in natural soil fabrics: Smart and Tovey (1981) and Bisdom (1983) provide excellent reviews of the submicroscopy of the mineral components.

Physical dimensions of specimens

Theoretically, the early stages of organic matter broken down to particles of micron size can be studied by light microscopy using thin sections of soil but practically, section thickness and the presence of opaque minerals and organic matter limits resolution to about 5-10 microns. The use of conventional heavy metal staining methods and TEM of ultrathin sections has allowed the detection of particles down to nanometer sizes *in situ* in natural soil fabrics (Foster and Martin 1981). At these sizes, however, except where the organics have a distinctive structure (membranes, microfibrils *etc.*) it is difficult to distinguish between organic and inorganic particles. Bisdom (1983) summarises the application of more sophisticated techniques for the identification of materials in soil samples, (ion microprobe mass analysis (IMMA), secondary ion mass spectrometry (SIMS), laser microprobe mass analysis (LAMNA *etc.*) which may be useful in distinguishing between organic and inorganic amorphous materials. Such sophisticated techniques are not generally available to soil scientists, however, so I have used ultracytochemical techniques to investigate the biochemical properties of the small fragments of organic matter *in situ* in soil fabrics.

SEM specimens may be up to 1 kg in size, but the area sampled in an electron micrograph depends on magnification and is usually quite small. For CTEM and STEM specimen size is limited by the distance fixatives and embedding media will penetrate. Blocks of soil only 0.5 - 1 mm cubed give the best results. The actual sections are 0.5 x 0.5 mm and 0.1 μm thick.

Physical and chemical stabilization of the soil fabric

Various components in plant and animal materials are naturally held together to form tissues. Similarly, interlocking crystals hold sections of rock samples together. Soils, on the other hand, are composed of randomly disposed and relatively widely spaced minerals, organic fragments and soil microorganisms lying free or only loosely interconnected. Hence, except for apical and sub-apical rhizospheres where the soil fabric is embedded in mucigel (Foster, 1981b; Campbell and Porter, 1983), before ultracytochemical analysis can begin, the soil must be stabilized both physically and chemically. Physical stabilization prevents relative movement of soil components during biochemical processes. It is achieved by embedding the soil sample in an amorphous gel such as gelatine or agar. Chemical stabilization prevents the loss of soluble components (lipids, low molecular weight gels *etc.*) during solvent exchange dehydration and is achieved with cross-linking agents such as aldehydes and/or polyvalent metals such as lanthanum. For ultramicrotomy the soil must be dehydrated and embedded in plastic (see Foster and Martin, 1981; Smart and Tovey, 1981 for details of techniques for soil specimens).

Ultracytochemistry

Ultracytochemistry is the detection and/or identification of (usually organic) materials in biological tissues by electron optical techniques. Here I use the term for any organic deposit whether part of a cell or free in the soil fabric. Ultracytochemistry has been used in biology for more than 30 years. At its simplest, it merely consists of adding solutions of heavy metals (typically Os, Pb, U) to soil samples. These react with, or are absorbed onto organics so that in ultrathin sections (50 nm - 100 nm thick) where they were previously electron transparent (and therefore invisible) they become electron opaque and so readily detectable.

Techniques for specific complex molecules.— Ultracytological techniques have the advantage that specific complex macromolecules with well defined biochemical properties can be detected and located *in situ* in a soil fabric section with a resolution measured in

nanmometers. For example, histochemical methods have been devised for examples from every major group of enzymes (Hayat, 1975). All the methods used here are from Sexton and Hall (1978).

Techniques for particular chemical groups.— Hayes (1980) has suggested that examples of pure biochemicals such as particular lipids, proteins, polyphenols and carbohydrates which can be isolated from living cells may be very uncommon in soils. Instead, uncontrolled enzymatic reactions during cellular autolysis and chemical reactions between the lysates, soil minerals and pre-existing soil organics, produce random combinations of these materials to form unique complexes (*e.g.*, humates) which no longer closely resemble the biochemicals found in living tissues.

Fortunately most ultracytological reagents detect particular reactive groups *e.g.*, OsO₄ reacts with phenolic hydroxyls, alkyl groups, sulphhydryl groups (for groups derived from plant residues see Bland *et al.*, 1971) so that conventional aldehyde/OsO₄ treatment detects plant cell wall remnants and humic material. The acidic polysaccharides of mucins, bacterial and fungal slimes and root mucilages are stained with ruthenium red or lanthanum hydroxide (Foster, 1981b).

Where they are not present naturally, specific reactive groups can sometimes be experimentally generated by chemical pretreatments. Thus neutral carbohydrates are detected by partial lysis with periodic acid to generate aldehyde groups which are then labeled directly with silver methenamin (PAMS) (Pickett-Heaps, 1967) or *via* thiosemicarbazide with silver proteinate (PATSP-Thiery, 1967). These methods give electron-dense deposits with a characteristic structure so that carbohydrates can be detected even against a background of soil mineral fragments, and have been used to demonstrate carbohydrate coatings in clay fabrics (Foster, 1981a). Similarly, complex epoxides which occur in leaf (Brown and Holloway, 1981) and root cuticles are detected by iodination and addition of suitable silver compounds. Hence a wide range of biologically significant materials can be positively and specifically located in or on organic particles in soils.

Detection by specific removal.— Other organic materials can be located by noting sites where staining disappears if the section is treated with a solvent or an enzyme. Thus Heritage and Foster (in press) identified native S grains in sulphur bacteria in sections of waterlogged soil by their solubility in CS₂. Since specific, highly purified enzymes are available commercially this has some potential, but does not seem to have been applied to soil components other than recognisable tissues (*e.g.*, mycelial strands, Foster, 1981c).

SOURCES OF ORGANIC MATTER IN SOILS

Newly deposited materials

The most common material entering soils is carbohydrates derived from leaves, branches, bark fragments and fragments and floral parts (especially pollen), and from root mucilages, exudates, and ephemeral root tissues.

Materials from aerial organs.— Depending on the depth from which the sample is taken, leaf fragments retain much of their characteristic cellular structure even though their tissues have been invaded by microorganisms (Plate 1a, b). Autolysis before leaf fall results in the loss of cytoplasm in many cells, and release of vacuolar polyphenolics causes the cell walls to be impregnated with materials which make them more electron dense after heavy metal staining than would occur in the live leaf (Plate 1c). Pine needles often contain extensive deposits of polyphenols which partially occlude cell lumens and stain the cell walls (Plate 1a, b). Most of

the carbohydrates are quickly removed by microorganisms so the cell walls collapse onto the vacuolar contents (Plate 1d). Eventually only much convoluted, lignified cell wall layers remain and the origin of the material becomes indeterminate (Plate 1e).

Materials from Roots.— One of the more interesting facts to emerge in the last 10 years is that roots deposit large amounts of organic matter into the soil whilst they are still functional. Up to 30% of the photosynthate reaching the root may be released into the rhizosphere (Barber and Martin, 1976; Martin, 1977; Martin and Puckridge, 1981) as gels, exudates and lysates (see Rovira *et al.*, 1979, for definitions). Most classes of plant metabolites (sugars, amino acids, vitamins, proteins, lipids, hormones *etc.*) have been isolated from root exudates (Rovira, 1965) but these are not preserved in preparation for electron microscopy. However they support bacteria and fungi (Plate 2a, b) which colonise the complex carbohydrates secreted by the root in the form of mucilages and proteins (*e.g.*, enzymes). In some cereal crops more carbohydrate may enter the soil as root mucilage than is stored in the grain as starch, (Samtsevitch, 1965). For example White (1983) estimates sloughed cells and gel amount to 3.5 tonnes/ha/yr for wheat.

Direct evidence from electron microscopy (Plate 2a) (Foster, 1981b; Foster *et al.*, 1983; Campbell and Porter, 1982) and theoretical calculations (Newman and Watson, 1977; Gardner *et al.*, 1983) suggest that these materials are mainly confined to the immediate vicinity of the root (0 - 150 μm). Tan and Nopamorabodi (1981) found a sharp break in P distribution between 200 - 300 μm from the root surface which may also indicate the outer limits of the rhizosphere gel. Using quite independent ultrastructural techniques Campbell and Porter (1982) and Foster (1981b) showed that there was an inner layer of mucilage near the cell surface (Plate 2a, b) which was much more dense than that 20 - 50 μm away; so, there may be partition of root products with distance from the root on the basis of molecular weight. Carbohydrates are neither preserved nor stained by conventional biological preparation techniques (Foster and Martin, 1981) but the acidic carbohydrates are preserved and stained by lanthanum hydroxide (Plate 2a) and the neutral carbohydrates by the PATSP (Plate 2b) and PAMS reactions (Plate 2c). These electron micrographs of known plant materials serve to calibrate these cytological tests for non-rhizosphere soils to be presented later.

All these root-derived organics are available to those animals such as collembolans, nematodes and enchytraeid worms which browse along roots (Head, 1967). At first, root mucilage may be enclosed by a cuticle (Greaves and Darbyshire, 1972), but this is soon ruptured (Foster, 1981b) allowing the gel to penetrate into the soil fabric. Mucilage appears to be a true gel, allowing water and ions to diffuse through it in a manner not significantly different from that in free water (Greenland, 1979). Although most of the root gel is secreted by the root cap, epidermal cells and root hairs also secrete mucilage. In drying soil, this may hold soil firmly to form a rhizosheath (Wallstein and Pratt, 1981). At first, colonies of bacteria develop in the soil surrounding the root in response to exudates penetrating the soil fabric. Later, bacteria and fungi attack the gel, especially along the grooves between the epidermal cells, leaving lysis holes (Plate 2a, b, c) in the mucilage.

In some semi-permanent grasslands, 53 - 98% of the standing crop is below the ground, and some grasses show a 100% root turnover each year (Dickinson, 1982) amounting to 5000 kg dry matter/ha/y (Whitehead *et al.*, 1980), so root tissues may be a considerable component of the annual organic matter input into soils. Little wonder then that Curry and Ganley (1977) found 89,000 microarthropods/sq meter, 80% being acarines and collembolans. Recent work has shown that death of the root cortex is a normal phenomenon unassociated with disease (Henry

and Deacon, 1981, van Vuurde *et al.*, 1979). Materials released by the death of cells causes a population explosion amongst the root surface microorganisms. Thus van Vuurde *et al.* (1979) found that in root segments 4 - 5 days old, where 35 - 45% of the cells were dead, supported a 1 - 4% microbial cover. When 45 - 75% of the cells were dead, (segments 7 - 8 days old), microbial cover increased to 8% of the root surface area.

Animals and their remains.— Most larger animals (here $> 1\text{mm!}$) escape during preparation, though nematodes may be observed in dead root fragments (Plate 3a), and soil ingesting animals recognised by clay and organic particles in their gut (Plate 3d), are occasionally encountered. The most common animal remains in ultrathin sections of soil are exuviae fragments and cast off appendages (Plate 3b, c, e, f). These are identified by their characteristic structure, ultrastructure and histochemical reactions (Foster, 1978; Foster and Martin, 1981). Live animals most commonly observed in soil sections are microorganisms such as amoebae and ciliates, (Plate 3 g, h) *etc.*

The abundance of soil animals in the surface layers of soils means that fecal pellets are of common occurrence, but they are not necessarily all derived from soil inhabiting animals; in some forests there is an almost continuous rain of pellets released by phytophagous insects in the canopy. Fecal pellets are recognised in SEM by their characteristic size and shape and some can be attributed to particular species. In TEM, fecal pellets and their fragments are easily recognised because their high enzyme and/or mucin contents make them stain strongly with heavy metals. The chaotic arrangement of their contents is characteristic, and often they contain cellular materials which are so little altered by digestive processes that cellular organelles (such as the thylakoids of chloroplasts) can still be recognised (Plate 3i). Many pellets contain bacteria, or support bacterial colonies in the surrounding soil (Foster *et al.*, 1983).

Further microbial breakdown.— Once incorporated in the soil, rapid degradation of tissues occurs through the action of plasmodia, fungi and bacteria. In turn, fungal hyphae are broken down by bacteria (Kilbertus and Reisinger (1975). Resins and polyphenolics from pines may be deposited in the soil (Foster and Marks, 1967). Kilbertus and Reisinger (1975) examined the stages in breakdown of leaf litter at the ultrastructural level. In clay soils most bacteria are associated with organic matter (Plate 4a - d). The larger bacteria are associated with cell wall remnants which still contain carbohydrate (electron transparent materials) (Plate 4a, c), but throughout the humified organic matter and even in the mineral rich parts of the fabric, there are many small microorganisms, many $3\text{ }\mu\text{m}$ in diameter (Plate 4a, b, d). Gradually organic and mineral soil components become intimately mixed. Firstly clay platelets become absorbed onto the gels secreted both by roots (Plate 2c) and bacteria (Plate 5a, b). Secondly fungal hyphae, root hairs and pieces of plant cell walls tens of microns in length become enclosed in extensive clay fabrics several microns thick (Plate 5c, f, g). The same is true for amorphous materials (Plate 5d, e, h, i). These materials will be physically protected from microbial attack until they are ingested and broken open in the alimentary tract of soil animals. They constitute part of the physically protected organic pool in soils.

Secondary sources of organic matter in soils

Microbial tissues and their secondary metabolites.— All the materials previously mentioned are further modified by microorganisms. Bacteria, actinomycetes and fungi are the most commonly encountered microflora and their lytic activities may be a prerequisite before tissues become available to soil animals.



Plate 1. Primary sources of soil organic matter – leaves. (a). Although most of the tissue has been replaced by microorganisms, the thickness of the cell wall indicates that the tissue was a leaf epidermis. (b). Detail of (a). The former cuticle is occupied by hyphae. The cell lumen is partly occluded by tannins(T). (c). Later stage of decay-only polyphenol rich cell wall remnants remain. (d). Most of the electron transparent carbohydrates have been removed from the cell walls so the cells have collapsed onto the vacuolar tannins(T). (e). Highly decomposed leaf tissue from a waterlogged pasture. Only distorted, humified cell wall layers remain.

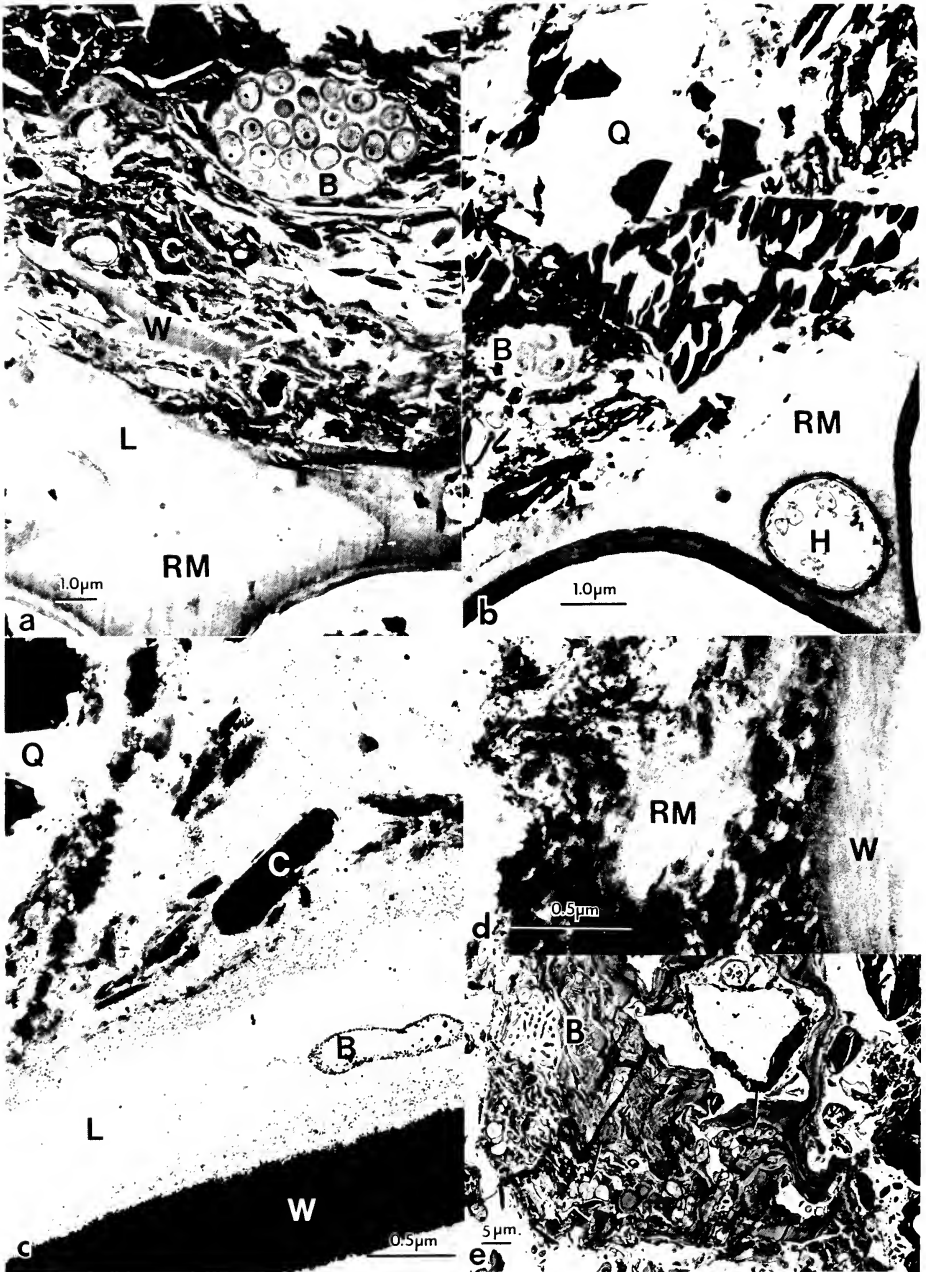


Plate 2. Primary sources of organic matter—roots.— (a). Lanthanum hydroxide reacts with substituted carbohydrates in the root surface mucilage (RM) which has been partially lysed (L) by soil bacteria. The mucilage holds cell wall remnants (W), clay particles (C) and a colony of bacteria (B) onto the root surface. (b). Neutral carbohydrates in the root mucilage (RM) are demonstrated by the PATSP technique. The gel and exudates support colonies of bacteria (B) near the root. Quartz grains (Q) shatter during ultramicrotomy. (c). The cell wall of both root (W) and bacteria (B) are intensely stained by the PAMS reaction but the root gel is only lightly stained. Clay particles (C) and quartz grains become embedded in the gel which is locally lysed by bacteria (L). (d). Even where root mucilage (RM) is separated from the root (W) by clay it can be recognised by its characteristic granularity and reaction with ruthenium red/OsO₄ complex. (e). Extensive decay by colonies (B) and individual microorganisms (arrows) leads to the collapse of the root tissue.



Plate 3. Soil animals and their remains.— Soil animals which play a major role in organic matter mineralization. (a). Nematode (?) in dead root fragment. (b). Appendage with live cells. (c). Empty appendages. (d). Soil ingesting nematode (?) showing several sections of the gut (G) with clay particles and organic matter. (e), and (f). Cast off and partially broken down insect parts. (g). An amoeba (A) in an organic rich surface soil. (h). A ciliate attached to a rhizomorph. (i). A fecal pellet (FP) recognised by its chaotic and electron dense contents, supports bacteria (B). Note nearby cell wall remnants (arrow heads) and membrane systems (arrows).

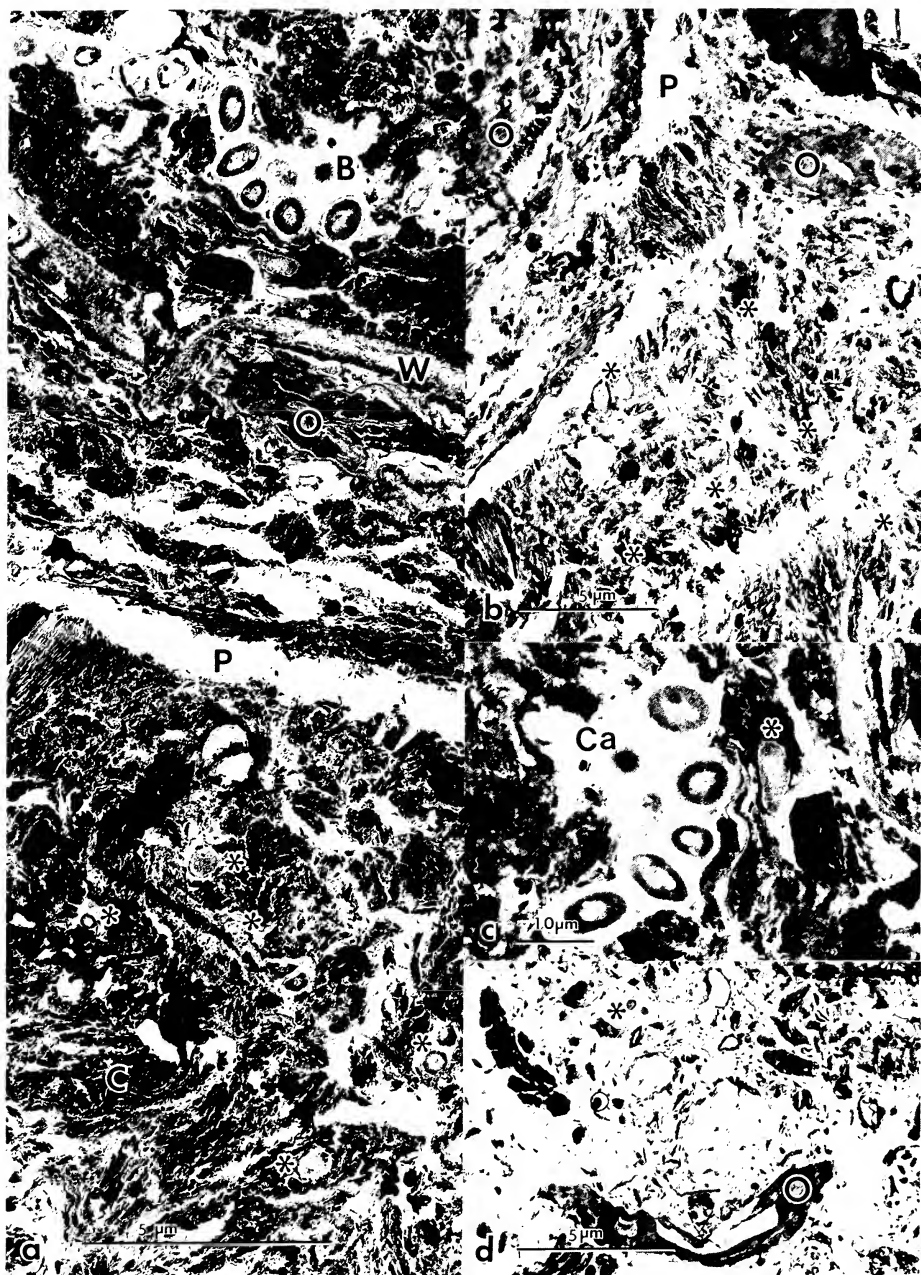


Plate 4. Soil fabrics with microorganisms and organic matter remnants.—(a). Bacteria (B) are usually associated with organic matter which still contains carbohydrate (eg. cell walls W). Other highly lignified and convoluted organic matter (O) does not support bacteria, but there are numerous microorganisms ($0.3\ \mu\text{m}$ diameter) scattered throughout the clay (*). P is a pore about $1\ \mu\text{m}$ in diameter. (b). Similar to (a). (O) is amorphous organic matter. Again there are numerous small soil bacteria in the clay (*). (c). Detail of (a) showing bacteria enclosed in capsule material (Ca) which is not stained by OsO₄. (*) indicates a capsule-less bacterium enclosed in humified organic matter. (d). A less consolidated clay fabric containing remnants of cell wall remnants (O) and an occasional microorganism (*).

Skinner *et al.* (1952) estimated that conventional plating techniques used by soil microbiologists only detected between 0.1 and 1% of the organisms present. Moreover according to Bae *et al.* (1972) more than 63% of soil microorganisms are less than $0.3\ \mu\text{m}$ in diameter and so not readily seen by light microscopy. Campbell and Rovira (1973) showed that because bacteria were enclosed in gel they are not readily detected by SEM and TEM of thin sections is necessary to clearly see all the microorganisms in a soil and to determine their probable viability (as indicated by their cytoplasmic ultrastructure).

The abundance of mucilages and exudates in young rhizospheres stimulates the growth and division of bacteria, fungi and actinomycetes both in and around the root. The more readily available exudates are used by less specialised bacteria such as the fluorescent pseudomonads which are particularly common in rhizospheres. A host of fungi, epiphytes, symbionts, cortical and stelar parasites, then colonise the roots and rhizospheres. These are followed by saprophytes, and together with bacteria, they remove the less resistant polymeric materials. Using electron microscopy, Foster and Rovira (1976) showed that a consortium (White, 1983) of different microorganisms were involved in removing different chemical fractions of the cell wall. Later, actinomycetes and bacilli become more abundant; these are able to attack more resistant materials such as lignified secondary walls of tracheids, sclerenchyma *etc.* Rhizosphere microorganisms reach population of $1.2^{10}\ \text{E}+10/\text{cc}$ of rhizosphere soil at the rhizoplane (Foster and Marks, 1967; Malajczuk, 1979) and attract not only other microorganisms (flagellates, amoebae, parasitic bacteria and viruses) but also larger animals such as mites, collembolans, nematodes *etc.* As well as feeding on the rhizosphere microflora, these may also remove the partially decomposed cortical tissues leading to the complete decortication of the root (Head, 1967).

Many of the exudates and lysates escaping from roots are used by the microorganisms in respiration and growth, but some microorganisms secrete new organics which act as secondary sources of energy for other soil inhabitants. With the development of the rhizoflora, microbial gels become inextricably mixed with the root-derived gels so that they are no longer morphologically or biochemically distinguishable: this complex colloidal carbohydrate mix was named mucigel by Jenny and Grossenbacher (1963). Mucigel and microbial polysaccharides have an important role in stabilizing soils (Martin, 1971; Forster, 1979; Gaspari-Mago *et al.*, 1979). Silt sized particles are bound to form larger aggregates by fungal hyphae. Clays become bound onto the surface of small colonies of bacteria both in the rhizosphere (Foster and Rovira, 1978) and bulk soil (Kilbertus and Reisinger, 1978). Some microbial gums are particularly resistant to breakdown (Greenland and Oades, 1975). Even after the death of capsule-producing bacteria, the carbohydrate fibrils may persist in the soil, (Plate 6e) binding the various mineral and organic components of soil crumbs together (Foster, 1981d; Foster *et al.*, 1983). Turchenek and Oades (1978) consider that, within aggregates, bacterial gel is the most important stabilizing agent as it binds clay particles into silt sized aggregates (Plate 6e, g). The binding action of microbial gels varies with the concentration of uronic acids (Martin and Aldrich, 1955).

The rhizosphere microflora Some fix nitrogen; others affect total root length, frequency of laterals, number, length and distribution of root hairs, number of layers in the root cortex and hence root diameter (see Foster, 1984, for review). As well, rhizosphere products release P, K, Fe *etc.* from insoluble minerals (Moghimi *et al.*, 1978).

Except in the surface layers where all the soil may come under the influence of the root, roots may occupy less than 6% of the soil volume. Elsewhere, organic energy sources are

confined to local remnants of organic matter, but despite the oligotrophic conditions in the non-rhizosphere (bulk) soil (Pointdexter, 1981), there are still large populations of microorganisms ($10^9 \text{E} + 9/\text{gm}$), and Clarholm and Rosswall (1980) show that in forest soils their numbers are more than sufficient to account for nearly all the organic C accession each year, and they consider that even under the most favourable conditions, only 15 - 30% of the bacteria were active. Although microbial populations in soil are so large, bacteria occupy less than 0.01% of the total soil surface (Grey *et al.*, 1968). They are not randomly distributed in soils, but are usually associated with substantial organic matter deposits. Thus, Gray *et al.* (1968) showed that in a sandy soil, 60% of the bacteria were attached to organic particles even though these composed only 15% of the soil volume. Similarly in large-area, ultrathin sections of soils Foster *et al.* (1983) showed that the larger (.5 - 1 μm diameter) microbial cells were associated with cellular debris which still contained carbohydrate (Plate 4a, b). Bacteria were also associated with highly lignified materials and occurred sparsely scattered in clay fabrics, but these cells were generally much smaller in diameter (0.3 μm diameter) and contained less stored food reserves such as polyhydroxybutyrate and polyphosphate than similar cells in the rhizosphere (Foster, 1978).

In an extensive ultrastructural study of a single aggregate, Kilbertus (1980) showed that within aggregates bacteria occurred within three different types of pore, those with single openings, those with multiple openings and those which were totally enclosed. He also showed that a minimal size of pore could be colonised by bacteria which bore a constant ratio to the diameter of the microorganism. Bacteria within the aggregates greater than 2 mm may experience anaerobic conditions (Greenwood and Goodman, 1967).

Bacterial gels and microbial slimes are recognised by their fibrous (Plate 6b) or granular (Plate 6c) texture, but extensive tracts of amorphous non-Os reactive gels are found in some soil sections (Plate 6a). These may be secreted by earthworms.

Some fungi deposit resistant substances such as melanins in their walls. As well as ribosomes rich in N and P bacteria may deposit storage materials eg. lipids, polysaccharides and polyphosphates in their cytoplasm. The rhizosphere microflora becomes a valuable secondary resource for the soil microfauna. Microfloral use of simple sugars in root exudates causes immobilization of inorganic nitrogen. It has been shown using "microcosms", (small plants growing in a defined medium to which bacteria, amoebae, flagellates, nematodes *etc.* can be added singly or in combination), that addition of predators and browsers, especially mites and nematodes, markedly increases that amount of nitrate nitrogen available to the host plant (Wood *et al.*, 1982; Elliot *et al.*, 1979). Chakraborty *et al.* (1983) showed that soil amoebae attack *Gaeumannomyces* hyphae so they may be important in the biological control of soil borne plant pathogens.

ORGANICS OF SUBMICRON SIZE

By the time many organic fragments are reduced to micron and sub-micron size they may be so modified morphologically and biochemically that their origin may be obscure. They are then best classified by their ultrastructure and histochemistry. Other particles may retain sufficient characteristic fine structural features that their origin is more certain.

Fibrous or lamellate materials

Many plant cell walls are composed of alternate carbohydrate-rich (electron-transparent) and lignin-rich (electron-dense) lamellae so wall fragments can be recognised on the basis of their distinctive multilamellate structure even when the fragments are less than 1 μm wide, (Plates 5c, g, 6d). Remnants of terminal and middle lamellae are characteristic in their dimensions, texture and electron density and are relatively resistant to decay (Plate 5f, i). As carbohydrate is removed from cell wall fragments and phenolic hydroxyl groups are unmasked, the remnants take up more and more metal ions either from the soil solution (*e.g.*, Mn Fe Al) or from electron dense stains and appear progressively more electron dense. Removal of the carbohydrates brings the electron dense lignin rich lamellae closer together. Finally only the lignin skeleton remains, distinguishable by its osmophilic, fibrillar structure.

In contrast, fibrillar remnants which do not react with Os but which are demonstrated by PAMS, PATSP or Au-labeled lectins may be recognised as filamentous polysaccharides such as cellulose microfibrils from higher plant cell wall remnants, or fibrils from the extracellular polysaccharide (ECP) layers of bacteria, actinomycetes or fungi. Some root surfaces are naturally fibrillar (Leppard and Ramomorthy, 1975; Roland, 1971) and Foster (1982) showed that in later stages of decay fibrils from internal cell wall layers are exposed by microbial or physical weathering and make contact with nearby soil minerals.

"Amorphous" or granular materials

Many materials which appear amorphous by light microscopy appear to be granular at the higher resolution of the TEM, especially after suitable histochemical treatment.

Carbohydrates.— Granular deposits in soil fabrics revealed by ruthenium/OsO₄ or La(OH)₃ are probably microbial gels or remnants of root mucilages. In their freshly-formed, fluid state, root mucilages flow freely into pores of submicron size in clay fabrics (Plate 2d) and if these pores are too small to admit bacteria they may be physically protected by the clay from microbial decay. Some of these deposits enclosed between clay tactoids are less than 0.5 μm across (Plate 8g, h) (Foster 1981a, Emerson *et al.*, in press), and although the individual deposits are of small volume, they may be numerous, and thus contain significant energy resources. Other materials reactive to PATSP or PAMS are associated with bacterial walls (Plate 7a, c, g) or are the remains of cell-wall materials of higher plants (Plates 6g, d), but other deposits are not associated with morphologically distinct remnants (Plates 7c, d, 8f). These probably represent fragments of root or microbial ECP. Finch *et al.* (1971) and Griffin (1981) consider that carbohydrate gels can act as water reservoirs. Rovira and Greacen (1957) and Powlson (1980) showed that physically disturbing soils increase their respiration. They proposed that grinding brings bacteria into contact with organic matter from which they were previously physically separated. It is not clear whether mere grinding would be sufficient to expose sub-micron sized deposits. Conformational changes due to dehydration or heating, (as in Australian surface soils), may further reduce the susceptibility of these deposits to decay, and according to Emerson (1977) when polysaccharides are bound to clays they become less susceptible to periodate oxidation. Both sectioned material and isolated clay particles show a very patchy reaction to PAMS (Plate 7d - f) but whether negative reactions are due to absence of carbohydrate or to their stabilization on the clay is not clear at present. The complete mineralisation of carbohydrates in and on clays probably depends on their release by grinding in the gizzards of such soil animals as earthworms.

Rybicka (1981) states that periodic acid used in the PATSF reaction specifically oxidises the 1, 2-glycols in polysaccharides to form aldehydes which subsequently react with thiosemicarbazide. The thiol group then reacts with silver to form an electron dense conjugate. The reaction has been widely used in the biomedical sciences to locate carbohydrates, but only rarely on studies of decomposition of organic materials in soils (Foster, 1981a).

The extracellular polysaccharides (ECP) of fungi and bacteria, whether they are granular or fibrillar, can be distinguished by their different resistance to periodate hydrolysis. By treating serial sections of the same soil fabric with periodate for different times before applying the PAMS reagent, Foster (1981a) showed that fungal ECP's were more resistant than those produced by bacteria or roots. Similarly, by incorporating ^{14}C -labeled bacteria and fungi into a grassland soil, Nakas and Klein (1979) showed that bacterial cell walls and polysaccharides were more quickly mineralised than those of the fungi. This may explain why carbohydrates under pastures (rich in root mucilages and bacterial ECP) are more susceptible to periodate degradation than those under forests (Clapp and Emerson, 1972), where most roots are mycorrhizal. Foster (1981c) found that enzymes that removed the cell wall polysaccharides from the thick-walled hyphae of mycelial strands from a forest soil failed to remove the ECP (Plate 8d, e). This may mean that fungal gels are less readily available to soil animals.

Humic substances.— With the fragmentation of cells, polyphenols from cell walls (Harkin 1967) and vacuoles (Zucher, 1983) are released into the soil, so that rhizosphere soils are richer in polyphenols than the bulk soil (Bokhari *et al.*, 1979). Several studies have shown that catalytic polymerisation of phenolic materials by clay minerals occurs to form materials with the properties of humic and fulvic acids (Wang *et al.*, 1980), and humic materials account for 60 - 70% of soil C (Griffith and Schnitzer, 1975). The importance of these products lies in the N they contain. Ladd (1981) labeled medic plants with both ^{14}C and ^{15}N and showed that 15 - 20% of the ^{14}C was still unmineralised after 4 years but nearly 50% of the ^{15}N remained as stable organic residues. Granular deposits in soils which stain densely with Os, U or Pb are probably "humic" materials rich in polyphenol/protein complexes (Plates 7h, 8g). These may be remnants of vacuolar polyphenolics but they may also represent secondary products of soil microorganisms (Tan *et al.*, 1978), or result from chemical weathering of such materials. Remnants with similar form, internal structure and staining properties as small as tens of nm have been seen in ultrathin sections of soils. These are probably to be identified with humic materials. Early work showed that humic materials formed spheres 60 - 100A in diameter (see van Dijk, 1971, for review). However Chen and Schnitzer (1976), Ghosh and Schnitzer (1982) and Stevenson and Schnitzer (1982) have shown experimentally that the precise ultrastructure of humic compounds *e.g.*, fulvic or humic acid) depends on such environmental factors as pH, water potential and salt concentrations. Thus, the same material may be deposited as sheets, bands or fine fibrils depending on pH (Schnitzer and Kodama, 1976) and this is probably true of similar materials in soils. It might be instructive to fix subsamples of the same soil fabric with aldehydes buffered to different pH's and to observe any difference in form of humic materials. Localized drying, secretion of H^+ ions by roots, or presence of carbonates may cause different deposits of the same material within a few microns of each other in the same soil fabric to have different forms! However it is probable that in nature most humic materials are complexed with clays.

Unfortunately, most of the humic materials in soils cannot be described in precise chemical terms, either because the existing techniques are inadequate for their separation and characterization, or because no two humic molecules are exactly alike (Oades and Ladd, 1977).

Design of specific ultracytochemical techniques is therefore impossible.

Membrane systems

It is not unusual to come across membranes in soils. These are 7 - 10 nm thick and are of variable length. Some are rolled into open or closed tubes and vesicles (Plate 3i (arrows)). These are probably cytoplasmic membranes released from living cells or when bacteria are lysed by bacteriophage. Most cellular membranes contain enzymes; it is possible that whole suites of enzymes, necessary for a sequence of biosynthetic steps which give rise to complex molecules, are preserved *in situ* in such membrane fragments, especially if the membranes roll up or form enclosed vesicles. Such membrane systems may be sites of quite complex biochemical transformations and could give rise to complex nutrients for soil animals.

Enzymes

Martinez and McLaren (1966) remark that, although hundreds of reports dealing with soil enzymes have been published, the question of the origin and localization of these enzymes is still as obscure as it was in the first decade of this century. Burns (1982) has proposed 4 main sites: (1), in the biomass; (2), inside or adsorbed onto cell wall fragments; (3), adsorbed in or on clay minerals; and (4), adsorbed onto or as co-polymers with humic materials. There has been a considerable discussion in the literature as to whether enzyme contents of soils correlate closely with microbial biomass (Nannipieri *et al.*, 1983) or not. Most classes of enzyme have been isolated from soils (Skujins, 1976) but their precise location in soil fabrics is unknown; therefore, the ratio of soil transformations associated with the biomass and with "free" enzymes remains undetermined.

Both roots (Plate 8a) and many soil bacteria excrete enzymes extracellularly where they are associated with their ECP's. (Plates 6b, c, 8b, c). It is also known that enzymes are stabilized by adsorption onto clay surfaces or by forming complex co-polymers with polyphenols. In experimentally synthesized enzyme/polyphenol co-polymers, the enzymes retain much of their catalytic activity and it is likely that similar co-polymers are generated during cellular lysis or after the release of their components into the soil. Enzymes in these complexes may be protected from the action of proteases released by nearby soil microorganisms. Non-enzyme proteins will also be preserved in these sites and may play an important role in animal nutrition.

Although *in situ* ultracytochemical tests for enzymes in soil fabrics have been successfully used to locate enzymes associated with microorganisms (Plate 6b, alkaline phosphatase: Plate 8b, acid phosphatase, Plate 6c catalase, Plate 8c peroxidase) and cellular debris (Plate 6h, acid phosphatase)(Foster, 1981d, 1982), unfortunately, they have so far failed to locate enzymatic activity in or on soil minerals. Some mineral fragments appear occasionally to have unusual electron-dense deposits associated with them after ultracytochemical tests, (Plate 8, b lower arrow). However, because enzyme histochemistry is generally performed on the bulk soil sample, it is impossible to perform experimental procedures and control procedures on adjacent serial sections by present techniques. Moreover since the sections are so thin and the deposits so small (10 - 100 nm) EPMA could not have been used to determine whether the electron dense deposits were fragments of electron dense minerals, or enzyme-specific heavy metal precipitates, so the specificity of these deposits was difficult to establish.



Plate 5. Physically protected organic matter.— (a), and (b). Clay is adsorbed onto the capsule of microorganisms. (c). Fragments of wall material (O) become enclosed in clay aggregates and hence protected from microbial decay. (d), and (e). Humified materials enclosed in a pore within an aggregate. The material appears granular at high magnification (e). (f), and (g). Amorphous (f) and lamellate (g) organic matter (O) enclosed in clay fabrics. (h). Amorphous organic materials mixed with clay. (i). Middle lamella fragment enclosed in clay.

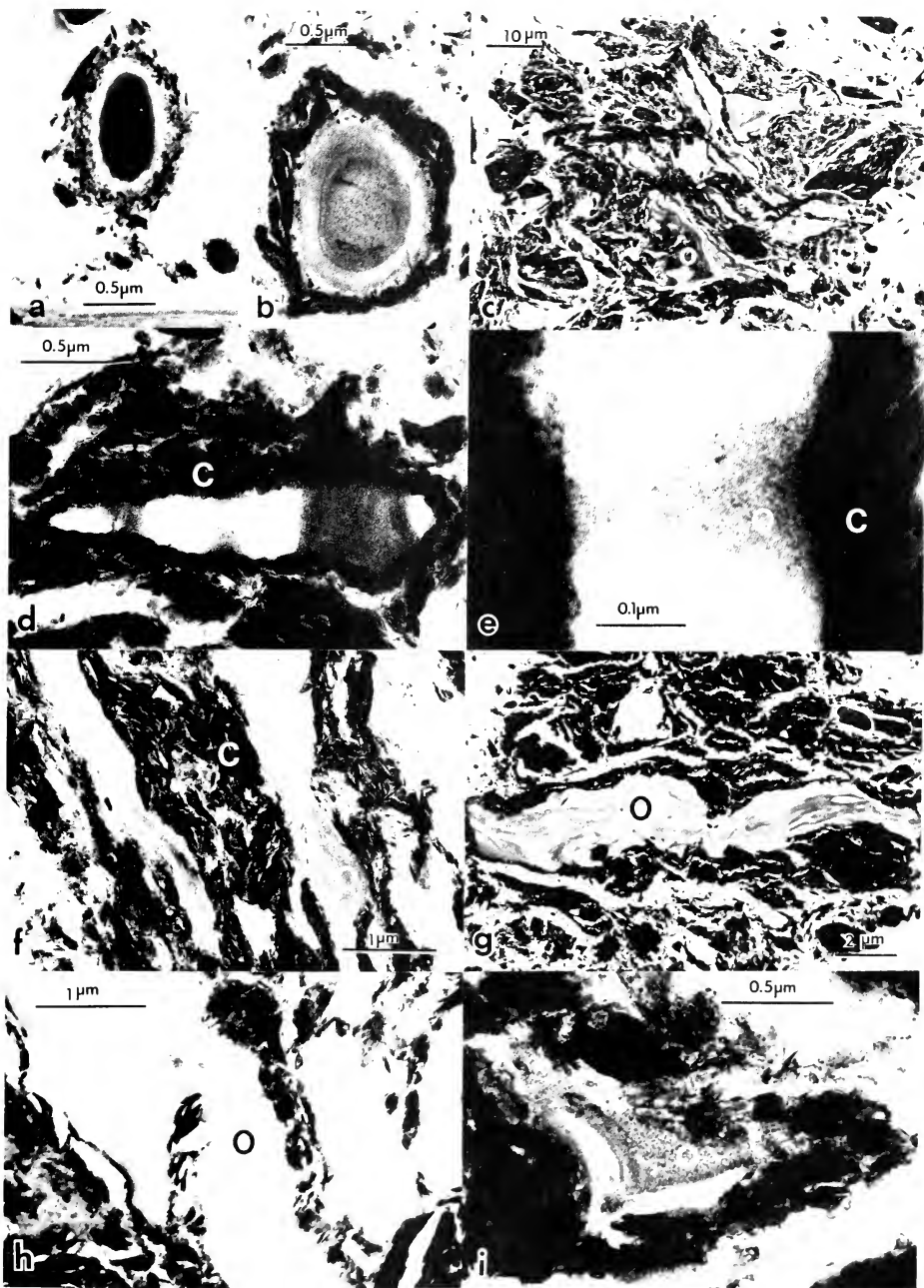


Plate 6. Acidic carbohydrates (lanthanum reactive) in soils. - (a). General view of a fabric containing amorphous (Ca) acidic carbohydrates and cell wall fragments. (b). Test for alkaline phosphatase locates the enzyme in microbial capsules. (c). Catalase is also associated with capsule materials. (d). Detail of (a) showing a small colony of bacteria (B) supported by amorphous and laellate organic matter (O). (Lanthanum stain). (e). Even after a bacterial colony (B) has died the capsule materials persist linking other soil components such as humic materials (arrow) together. (f), and (g). Fibrous (f) and amorphous (g) lanthanum reactive organic materials in clay fabrics (arrows). (h). After the acid phosphatase reaction some organic particles (O) appear to have to have enhanced electron density. (i). Membrane (arrows), possibly remains of plant cell walls abound in many soils.

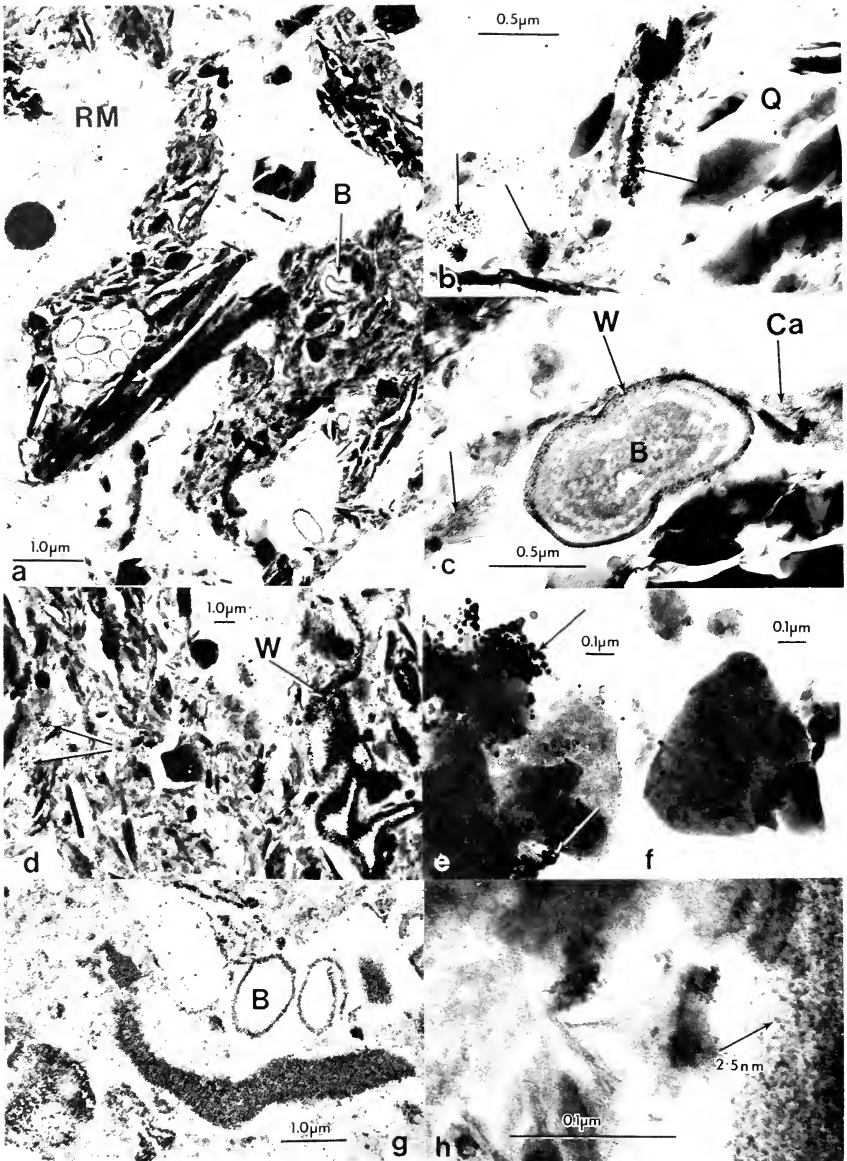


Plate 7. Neutral carbohydrates (PAMS AND PATSP-reactive) in soils.— (a). PAMS stains the cell walls of bacteria (B) but not their capsule carbohydrates or the root mucilage (RM). (b). At higher magnification the granular product of the PAMS reagents is associated with linear, presumably wall materials, round objects, perhaps bacteria and clay particles (arrows). (c). Similarly the PATSP reagents stain the cell wall (W) of bacteria (B) as well as amorphous materials (Ca, arrow) in the soil. (d). Wall (W) and other organic deposits stained by PAMS. (e), and (f). If clay particles are isolated from soils and tested with the PAMS reagents only certain particles are stained (arrows), as when sections are stained. This suggests that only a few clay particles are coated with carbohydrate. (f) is the control which has been treated with silver methenamine but not with the periodate. (g). PAMS treated “humus” from a compost heap. The material varies widely in its reaction to the stain; presumably the particles which are less intensely stained are devoid of materials that are readily periodate-reactive. (B) indicates bacteria. (h). At high magnification os-treated materials contain granules 25 nm in diameter. These are probably humic materials.



Plate 8. Various histochemical reactions.— (a), and (b). In plant cells (a) acid phosphatase is associated with the plasmalemma and cell wall. In soils (b) acid phosphatase is generally associated with bacteria, though usually only a few react. Electron density is sometimes also associated with amorphous materials (lower arrow). (c). In waterlogged soils peroxidase is associated with narrow tubular microorganisms (arrows) though, again, only a few of the cells are reactive. (d), and (e). The thick walled hyphae of mycelial strands in soil stain intensely throughout (d) but if the cells are pretreated with amylase, only the outer layers of the cell walls still stain. (f), (g), and (h). The final product of organic matter transformations in soils are amorphous materials. These are usually mixed in composition since they stain with PATSP (neutral carbohydrates) (f), osmium alone (humic materials) (g) and ruthenium red/osmium (acidic carbohydrates) (h).

SUMMARY AND CONCLUSIONS

There are three reasons why ultracytochemical studies of soil organics are difficult. First, the hardness of minerals imposes severe technical restraints; second, electron micrographs are usually monochrome; and third, organic materials in soils are chemically complex and much modified from their original structural and biochemical properties.

Dommergues *et al.* (1977) consider that TEM is useless for quantifying materials in soils because of the sophisticated and lengthy procedures involved in sample preparation, and difficulties with respect to microscopic field orientation and size. The great resolution of the TEM has its premium in the extremely small area examined, so that where quantification may be attempted, sample variability is the dominant consideration. The role of TEM ultracytochemistry is, rather, investigation of the structure environment of organic matter at stages of mineralization which are determined by prior quantitative biochemical or biophysical studies.

Although image processing can be used to produce colored displays of electron images, *e.g.*, distinguish between electron density due to background osmium reaction and that due to an histochemical reaction on the basis of element distribution (Tanaka and Mitsushima 1984), most electron micrographs contain only black, white and grey areas. In general only those products which are electron-dense can be detected, *i.e.*, minerals and materials containing heavy metals. It is, therefore, much more difficult to design ultracytochemical reactions for electron microscopy than cytochemical reactions for light microscopy, where colored stains markedly enhance the visibility of the products of histochemical reactions. Ultrathin sections of most biological tissues have little or no intrinsic electron density, therefore, the results of histochemical tests are unequivocal, providing adequate controls are employed in which target groups are masked or destroyed. These ideal conditions do not hold for ultrathin sections of soils. Here the minerals are electron-dense to varying degrees; organic matter may adsorb electron-opaque materials from nearby minerals. Moreover, although histochemical reagents give unequivocal results when tested against relatively pure and well characterised materials in tissues, the same may not be true of the much modified materials which occur in soils.

Until recently, histochemical reagents were not very specific. The use of antibodies and lectins labeled with heavy metals, (Knox and Clark, 1978) may prove very useful in the study of mineralization of organic matter though preliminary experiments showed little sign of specific staining of rhizospheres (Foster, unpublished). Lectins may almost prove to be too specific in that they may detect only relatively unmodified materials which can be recognised anyway from their structure or location.

Ultrahistochemical analysis of soil fabrics is important because it provides information not easily obtained by other electron optical techniques. Thus ultracytochemistry not only tells us where organics are located in soil fabrics, but also something of their biochemical properties. EPMA, SIMS, LAMMA *etc.* are useful in that they tell us what elements, ions or chemical groups are present in organic deposits; they do not tell us how these parts are put together to form an organic complex.

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THE IMPORTANCE OF SOIL FAUNA IN REGULATING SOIL MICROSTRUCTURE AND SOIL MANAGEMENT IN FORESTS

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ABSTRACT

The effect of faunal activities on structure formation is most impressive in soils containing a dark humic horizon of the mull type (mollic epipedon). Especially in the transition zone to a brighter subsoil it can be shown, in which way aggregates of different origin are locally deposited, changed, and reincorporated in larger units or coherent areas. Shape and size make evident that various kinds of soil animals contribute to this cycling process, finally resulting in a complete contacting and mixing of organic and organic components and forming new mull.

In forest soils often the humic material does not reach the status of dark mull. In such cases it is often unclear how far the soil fauna is involved in the incorporation of organic substance into the soil. The study of thin sections by means of an incident light fluorescence-microscope can indicate that the transport and mixing effect in such soils is often underestimated. Small organic particles, invisible with other microscopic techniques, can be observed also in subsoil areas. Their spatial distribution is not to explain merely by root growing and rotting processes.

In forest management two factors which are related to soil structure are of particular importance.

The use of heavy machinery leads to increasing problems of soil compaction. Depending from the soil properties and the climatic conditions hydromorphic features may be formed. Leaching will cause an instability of the binding forces and the regulating potential of the fauna is often repressed.

The other factor is acidity. The humus horizons of acid soils onto podzols (spodosols) are well known. It is obvious that the structure forming activities are strongly reduced. We have to take in account, that possibly the processes leading to acid soil conditions are much faster today than supposed before. Meliorative measures will be discussed.

SOIL FAUNA AND AGRICULTURE: PAST FINDINGS AND FUTURE PRIORITIES

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ABSTRACT

General findings of soil: soil fauna research are given under the headings of soil pests, effects of beneficial soil animals, and effects of agricultural practices. Arguments are presented for a sustainable agriculture and for a more rational approach to problem solving within agroecosystems. The use of indicators of agroecosystem distress is advocated. Comments are included on research needs and implementation of sustainable systems of soil management.

RÉSUMÉ

Les découvertes générales de la recherche sur les sols et leur faune sont présentées sous les en-têtes d'organismes nuisibles, d'effets des animaux bénéfiques aux sols, et d'effets des pratiques agricoles. L'auteur offre des arguments en faveur d'une agriculture soutenable et d'une approche plus rationnelle pour résoudre les problèmes dont souffrent les agro-écosystèmes. Il préconise l'utilisation d'indicateurs de stress dans les agro-écosystèmes et commente sur les besoins en recherche et sur la mise en oeuvre de systèmes soutenable d'aménagement des sols.

INTRODUCTION

Agriculture is defined as the science or practice of cultivating the soil and rearing animals, and cultivation as the preparation, tillage and use of soil to produce crops. Because definitions aim to clarify and simplify meaning, they often perpetuate destructive myths that are harder to change than the definitions that incorporate them. The above definitions, for example, paint a picture of a linear agriculture with a black box, the soil, in the middle. The farmer stirs up the soil with a tool, sows seeds and harvests the plants that mysteriously grow. At first the system was thought to be limited to people, land, seeds and tools. More recently, synthesized fertilizers and pesticides have been added to the equation. These and other developments have led to an agriculture that is characterized by large parcels of land being kept bare for most of the year, often only one crop species being grown year after year, and production being maintained through a heavy reliance on imported seeds, energy as fuel for equipment, fertilizers and pesticides. The outcome has been increased dependence, environmental stress and a loss of capital from the system in terms of crop cultivars, soil and nutrients, water, natural controls of pests, and other beneficial organisms.

Studies of the relationships between soil fauna and agriculture have been conducted within such systems. They comprise three types of studies: (1), of pest species and their control; (2), of beneficial species and their effects; and (3), of the effects of agricultural practices on soil animals. Because of the difficulties of studying organisms in a stratified opaque medium that is complex in terms of its physical, chemical and biological parameters, and that varies in time and space, progress in all of these areas have been limited. Some general statements, however,

can be made. Useful reviews are provided by Kevan (1962), Edwards and Lofty (1969), Mills and Alley (1973), Wallwork (1976), and in the Proceedings of the Colloquium edited by Dindal (1980). As most of the following statements are of a general nature or are based on personal observation and/or on the soil fauna literature in general, they are not supported by specific references. These are, however, given where useful reviews or landmark papers are known to exist, or where particular points need to be stressed.

SOIL PESTS

1. Soil pests are at least as significant, in terms of economic damage, as above ground pests.
2. Pesticides, because of difficulties of distribution in soil, adsorption and decomposition, have provided less effective control in soil than above soil.
3. The biology and ecology of most soil pests is inadequately understood and relatively few biological controls have been exploited.
4. The use of cultural methods (crop rotation, use of intercrops, timing of operations, soil and habitat management) and resistant crop varieties, if available, are essential for the control of soil pests.

EFFECTS OF BENEFICIAL SOIL ANIMALS

1. All soil animals have beneficial effects on soil structure and fertility.
2. Although their direct effects on processes such as soil formation and organic matter decomposition are small in comparison with those of microorganisms, their indirect and catalytic effects are substantial and essential. These include the improvement of food and space conditions for microorganisms and higher plants, selective cropping and transportation of microorganisms, aeration, drainage, biological control of pests and soil mixing. Generally, their role should be seen as one of "regulation" rather than the simple acceleration of soil processes, which is a common misconception. (Macfadyen, 1961, 1963; Weetman *et al.*, 1972; Hill *et al.*, 1973; Behan and Hill, 1978; Lee, 1979; Anderson *et al.*, 1981; Luxton, 1982; Parkinson, 1983; Seastedt and Crossley, 1984).
3. Most studies of the contribution of soil animals have failed to deal with the soil system as a functional whole. Rather, they have focused on isolated groups and processes. Consequently our views of how the soil works is still very fragmentary.
4. Few attempts have been made to introduce and manage beneficial soil fauna (Edwards 1981). Developments in this area will eventually lead, together with parallel developments in other areas, to the redesign of our food producing systems and to changes in our approach to soil management.

EFFECTS OF AGRICULTURAL PRACTICES

1. Dominant agricultural practices (tillage, clean cultivation, monoculture, row crops, use of pesticides and certain synthetic fertilizers) simplify the soil community and reduce the beneficial contribution of soil animals (Edwards and Lofty, 1969; Edwards and Thompson, 1973; Andrén and Steen, 1978; Edwards, 1983). Manures and most fertilizers generally increase numbers and species of soil animals (Marshall 1977).

2. Although numerous studies have been carried out on these effects they have not led to any changes in agricultural practices - the beneficial soil fauna remains a largely unknown and untapped resource within the food system.

3. Preliminary studies have indicated the value of using the presence and population density of certain soil animals as indicators of soil conditions (Karg, 1968).

4. The growing concern with soil degradation and interest in minimum tillage and ecological approaches to agriculture are causing some attention to be focussed on the soil fauna (Stinner and Crossley, 1983). The questions that are being raised provide soil ecologists with an important opportunity to make practical contributions to the design of sustainable food systems.

SUSTAINABLE AGRICULTURE

As responsible scientists we have an important role to play in the evolution of a sustainable lifestyle for our species. Because of its increasing dependence on distant non-renewable and renewable resources, and its heavy environmental impact, modern agriculture is clearly not sustainable.

Systems of agriculture that have increased "productivity" (to satisfy markets manipulated through advertising), "profit" and "power" as their primary goals, are not sustainable and lead to the degradation of person and planet. This is because these goals know no limits. They are exhausting of resources and unresponsive to their harmful side-effects. What I am arguing for is a greater social conscience among scientists and a translation of that conscience into research that is relevant to food systems that have goals such as nourishment, fulfillment, flexibility, and sustainability (Hill, 1982; Hill and Ott, 1982; Hill, 1984a). I am also arguing for soil biologists and ecologists to speak out on these issues, and to broaden their area of interest to include the food system as a whole and its sustained operation over the long-term.

Let us now consider what a sustainable food system might entail and what contributions soil biologists can make towards its development and implementation.

In terms of material flows, a sustainable agriculture may be viewed as a production - consumption - recycle system. Most of the recycle process takes place within the soil in the form of organic matter decomposition. For sustainability to be achieved, inputs for decomposition must meet certain quantitative and qualitative criteria, *e.g.*, comprise a diverse range of substrates containing adequate amounts of major, minor and trace elements that, together with those from the earth's crust and the atmosphere, are capable of supporting plant growth. Substrates must also meet certain time, space and freedom from toxins, criteria. These criteria are more likely to be met in a multi-story polyculture that includes soil and ecosystem maintaining, as well as food producing, plants and animals, than in a uni-story row-crop monoculture (Mollison, 1979; Altieri, 1983; Todd and Todd, 1984). The agricultural task is the design and management of such systems and the soil zoology task is to describe the animals and processes that take place in the soil and, with others, to develop methods of soil management that can enhance the beneficial contributions of the soil fauna.

PROBLEM SOLVING WITHIN SUSTAINABLE AGROECOSYSTEMS

The approach to problems in such systems will probably differ radically from that employed today. Currently, agricultural problems usually receive attention only when their short-term

economic consequences justify the required expenditures. Solutions tend to be confined to disciplines rather than multidisciplinary: entomologists dealing with insects, nematologists with nematodes, and so on.

An alternative approach, recognizing that the causes of problems often lie outside of the discipline concerned with their subject, and that prevention is usually less costly than cure might channel the efforts and resources that currently are used to directly attack problems to a less easily defined, maintenance function for multifaceted agroecosystems. Thus, by working to optimize the functioning of the agroecosystem as a whole, problems within its parts would be minimized. Those that arise would be taken as indicators of malfunction, and efforts would be made to correct the malfunction. To be effective with this approach farmers would need to be more knowledgeable and, "closer" to the agroecosystem, and supported more by society. Sociologically the process may be viewed as one of integration (of our species into the rest of the biosphere), balance (the maintenance of a sustainable relationship with the support environment) and feedback (paying close attention to the outcomes of our actions, recognizing their meaning and responding accordingly). Thus, attention is shifted from problem solving to system maintenance, the incidence of problems declining as systems approach optimal states. Problems that do arise are solved largely by removing the causes and strengthening the natural processes that normally prevent such problems from reaching crisis proportions (Hill, 1984b).

INDICATORS OF AGROECOSYSTEM DISTRESS

Recognition of undesirable processes often involves the identification of environmental stressors and the detection and measurement of their effects.

Because of the widespread and diverse nature of environmental stressors, and because of the complex nature of their interactions, there is a need to find ways to detect and measure their combined effects in a general way. Influenced by Selye's (1946) recognition of a "biological distress syndrome" in mammals, Rapport (1983) has proposed that we recognize a parallel "ecosystem distress syndrome" within environments. This concept is based on two important assumptions: (1), that different stressors give rise to certain similar symptoms (cf. Selye's "general adaptation syndrome"); and (2), that there are common indicators of distress that can be used in widely different ecosystems subject to different stressors.

The situation in mammals, however, is much more complicated than Selye has indicated. Randolph (1976), uses five levels to describe recognizable points along a continuum from healthy to severe illness within affected humans. One valuable insight from his observations is that at different times the symptoms present themselves in "up" (e.g., hyperactive) and "down" (e.g., depressed) states. While these are both recognized as being undesirable at the developed end of the spectrum, during the early stages of development the "up" condition (active, responsive, enthusiastic, ambitious, witty) may easily be regarded as desirable, its connection with the "down" condition (stuffy nose, occasional coughing and sneezing, skin disorders, gas, diarrhea, constipation, frequent urination and various eye and ear symptoms) not being recognized.

There may well be parallels to these observations with respect to the soil ecosystem (Hill, 1980). Thus, certain management practices may at first appear to be beneficial when measured in terms of their short-term influences on productivity. The negative effects of these practices are either hidden or not taken seriously until they reach crisis proportions, when it may be too late to correct the situation.

The following indicators of environmental distress, identified by Rapport (1983) for the Great Lakes Ecosystem, are equally applicable to soil ecosystems:

1. Imbalance in nutrient concentrations (loss of some, accumulation of others)
2. Reduced species diversity
3. Replacement of longer lived by shorter lived species (adapted to transitory novel environments)
4. Replacement of larger by smaller life forms
5. Decline in biomass of macrofauna
6. Increase in amplitude of population fluctuations of key species.

Some of these were recently recognized by Andrén and Lagerfö (1983) in their study of the effects of various agricultural practices on soil mesofauna.

One problem with these indicators is that they only provide an after-the-fact indication of distress. This limitation similarly applies to many specific indicators of environmental contamination, such as the accumulation of toxins up the food chain, and the incidence of reproductive failure among top predators (Rapport, 1983).

In addition to these indicators, we urgently need others that are able to provide us with an early warning of deteriorating conditions. For this, Rapport (1983) has proposed that we identify "indicator-integrator" organisms, species that are representative of their communities, are able to survive only in relatively unstressed ecosystems, and that are sensitive to a broad range of stressors.

Among soil invertebrates, predators within the air spaces and water film and highly mobile burrowers would seem likely candidates for this role. Karg (1968) has, long ago, stressed the value of using predatory soil mites as indicators, and Greenslade and Greenslade (1983) make a similar case for using ants. Predatory nematodes would probably serve a similar function within the water film. In fact, all soil animals are indicators of soil conditions. The problem is the interpretation of the information provided. Predators are particularly valued because their presence, population density, behaviour and body composition can provide, in a sense, a summation of most of the information provided separately by the organisms lower down in the food web. Among the non-predators, earthworms are already widely regarded by farmers as indicators of soil health, and have been successfully used as indicators of soil pollution by pesticides and industrial chemicals (Edwards, 1979, 1980). Ghilarov (1965) and Krivolutsky (1975) have proposed using soil fauna as indicators of soil type. The person with the greatest need for this "indicator information" is the farmer, and researchers should keep this in mind.

While it is essential that more work be done in this area, experience from other fields is not encouraging with respect to the ability of such studies, on their own, to bring about appropriate changes in agricultural practices. While most human populations are willing to support studies of the side-effects of their behaviour, it is rare to find changes in behaviours as a result of such studies. I have observed that most people only want to hear truths that validate their present lifestyles, that do not cause them to feel guilt, and that do not suggest that they should change their behaviour. It is often implied that, as scientists, we are more objective and more willing to be open to truths that disturb, but this has not been my observation. I believe that most of us conduct our science (and our lives), just as non-scientists conduct their lives, within a territory determined by our vulnerability to the truths that are likely to distress us. This implies that by increasing our vulnerability we are likely to improve our science. This involves opening-up more to our colleagues, to those in other disciplines, to non-scientists and, in a somewhat different sense, to the subjects of our research. The fact that this meeting has taken place, bringing

together soil micromorphologists and soil zoologists from around the world, is a positive step in this direction.

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SOIL FAUNA AND SOIL STRUCTURE: FEEDBACK BETWEEN SIZE AND ARCHITECTURE

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ABSTRACT

The relations between soil fauna and soil structure are examined using papers from this conference as a background. Our synthesis focuses on function of the soil system and reciprocity between soil animals and other soil components.

Advancement of knowledge at this interface has been impeded by disciplinary specialization and isolation, and failure to frame hypotheses and research strategies in the context of the entire soil system. Two major challenges must be met before progress will be possible. First, philosophical beliefs about soil must be separated from objective science. The second problem is mainly taxonomic. For soil animals, problems of correlating phylogenetic and ecological groupings must be resolved. For soil micromorphology, classifications must be simplified and made more accessible to soil ecologists.

We conclude that soil animals regulate soil function through both trophic interactions and biophysical mechanisms which influence microhabitat architecture. The mixed culture aspect of soil communities involves diverse species interactions which regulate the structure of soil communities. We propose that comminution and disintegration of microstructures be added to formation of microstructures and comminution of plant debris as a third biophysical regulatory mechanism. This leads to a dynamic view of micropedology. Establishing links between groups of soil organisms and specific soil microstructures as seen in thin section will require substantial collaborative effort. Such efforts will yield basic information necessary for solving pressing applied problems in management of renewable resources depending upon soil.

RÉSUMÉ

Nous synthétisons les rapports entre la faune édaphique et la structure des sols à la lumière des articles présentés au cours de la conférence. Cette synthèse se concentre sur les fonctions des sols en tant que systèmes et sur la réciprocité des rapports entre les animaux édaphiques et les autres composantes du sol.

Le progrès des connaissances à ce niveau a été entravé par la spécialisation et l'isolement des diverses disciplines, et par le manquement à formuler des hypothèses et des stratégies de recherche qui considèrent les systèmes édaphiques dans leur ensemble. Deux défis de taille doivent être confrontés si l'on est pour progresser. D'abord il faut séparer les convictions philosophiques au sujet du sol de l'approche scientifique objective. Deuxièmement, il faut surmonter les problèmes taxonomiques. En ce qui concerne la faune édaphique, il faut réussir à corréler les groupes phylogénétiques avec les groupes écologiques. En ce qui concerne la micromorphologie des sols, il est nécessaire de simplifier les

classifications et de les rendre plus accessibles aux écologistes étudiant les sols.

Nous concluons que les animaux édaphiques régularisent la fonction du sol par des interactions entre les niveaux trophiques et par des mécanismes biophysiques qui affectent l'architecture des microhabitats. L'apparence de culture mélangée que présentent les communautés édaphiques met en jeu des interactions diverses entre les espèces qui régularisent la structure de ces communautés. Nous proposons que la pulvérisation des débris et la désintégration des microstructures soient considérées comme formant un troisième mécanisme régulateur biophysique en plus de ceux de la formation des microstructures et de la pulvérisation des débris végétaux. De cette façon on obtient une image dynamique de la micropédologie. L'établissement de liens entre les groupes d'organismes édaphiques et les microstructures spécifiques des sols requièrera des efforts de collaboration substantiels. De tels efforts permettront d'obtenir des informations fondamentales nécessaires pour résoudre les problèmes pratiques d'aménagement des ressources renouvelables qui dépendent du sol.

INTRODUCTION

As the circle of knowledge increases, so too does the fringe of ignorance. An objective of this conference was to increase knowledge without expanding the fringe of ignorance by combining results of analyses from two spheres: soil micromorphology and soil zoology. The mathematical proof of the above possibility is simple, but the challenge of bringing about constructive interaction between soil micromorphologists and soil zoologists is not.

Since the pioneering work of Kubiena (1938) we have known that soil structure and function are intimately related. In this conference, papers by Hill and Parkinson showed that soil animals regulate other soil biota both directly and by altering their environment. Altemüller, Mermut, Pawluk and Rusek showed convincingly that soil animals play a large role in organizing and maintaining soil fabrics.

Increased understanding of relations between soil fauna and soil structure will have important practical benefits. For example, Hill remarked that sustained agriculture depends on understanding the regulation of complex biological processes occurring in soil rather than indiscriminately accelerating a few. Several authors repeated the theme that soil animals contribute to soil quality and modify soil profiles and nutrient supply to agricultural crops. In particular, the paper by Edwards summarizes information now available about the importance of earthworms, a topic that was first studied experimentally by Charles Darwin (1881). Papers by Greenslade, Mermut, Pawluk and Rusek showed that animals generate structural units in soils from the Arctic through temperate regions to the tropics.

Despite immense opportunities for both basic and applied research, soil ecology has remained a relatively unstudied discipline. The generality of much ecological theory, developed from studies of freshwater and terrestrial systems, could be tested by work with soil systems. Also, working out the relationships among biotic and abiotic components of the soil can provide interesting proximate frameworks for research. Mechanistic questions about relationships between soil fauna and soil structure have been raised by most speakers. For example, both Dindal and Norton pointed out the apparent paradox of persistence of faecal pellets associated with increased rates of decomposition in the presence of soil animals. An important question, raised by Foster's presentation, is the extent to which soil animals are involved in disintegration of fundamental soil structural units. Resolution of such questions will increase understanding of the important but poorly understood decomposer food web.

In this paper we review some of the past impediments to interaction between soil zoologists and soil micromorphologists, develop the concept of the soil system as the unifying link between their disciplines, and present some ideas flowing from such a conceptual approach to studying relationships among soil animals and soil structure.

IMPEDIMENTS

In North America, soil morphologists and soil zoologists have not communicated in the recent past, in part due to a tradition of geological affinity of the former group and the predominant zoological background of those interested in soil animals. For both groups, the focus of attention frequently was not the soil but some small portion of it. It was therefore logical to communicate with those having similar interests. A shift of focus to the soil system would underscore the important point that soil zoologists and pedologists are working on the opposite side of the same coin. Effective soil ecology will depend upon increased cooperation between workers in these two areas.

It is true that the animal and its phylogeny or the organic-mineral complexes and their fabrics are important analytical frameworks in the respective spheres of soil biology and pedology. However, we suggest that while such perspectives facilitate analysis of parts of the soil system, exclusive commitment to these points of view has prevented synthesis. In the broader view, analysis without synthesis is a scientific dead end. Hoffman's comment that "myriapods are not just objects to be classified nor are they simply objects to produce faecal pellets" is appropriate.

Until recently, pedologists and soil zoologists have been necessarily preoccupied with description of immense natural diversity. The size of various groups of organisms, and the diversity of soils and fabrics has inevitably promoted disciplinary specialization. Unfortunately, it appears that with overemphasis on analysis, proximate goals of such specialization have become ends in themselves. We do not hold that further analytical work is either undesirable or unimportant. However, we are convinced that a general framework for synthetic work is available and that we can now proceed without waiting for more perfect descriptions of all components of the soil system. In fact, it is likely that descriptions will be improved by experimental studies of interactions among components and by information about emergent system properties that is generated through synthesis.

From information now at hand, some immediate requirements are obvious. Rusek pointed out the need to distinguish ecological groups of soil animals. This requires recognition of the reciprocity between soil animals and other soil components, and realization that soil animals are part of soil, not mere inhabitants of it. The idea is not new. In his review of the history of soil zoology, Kevan remarked that in 1757 Adamson recorded the reciprocity between termites and soil.

Real progress in science is probably often hampered by disciplinary boundaries which have been created mostly for the convenience of administrators. The willingness of scientists to adhere strictly to narrow administrative limits appears to be a recent development, even among workers interested in the soil. For example, Hoffman reported good work was done in the 19th century by people sharing their efforts among myriapods, echinoderms and mammals. A growing awareness of the reciprocity between soil animals and other soil components led to this conference and is reflected in a remark by Parkinson in his presentation: "Kubiena was remarkably perceptive both as a soil biologist and soil scientist - I suppose they are synonymous." Recognition of that unity is growing and is the central thesis of this summary and synthesis.

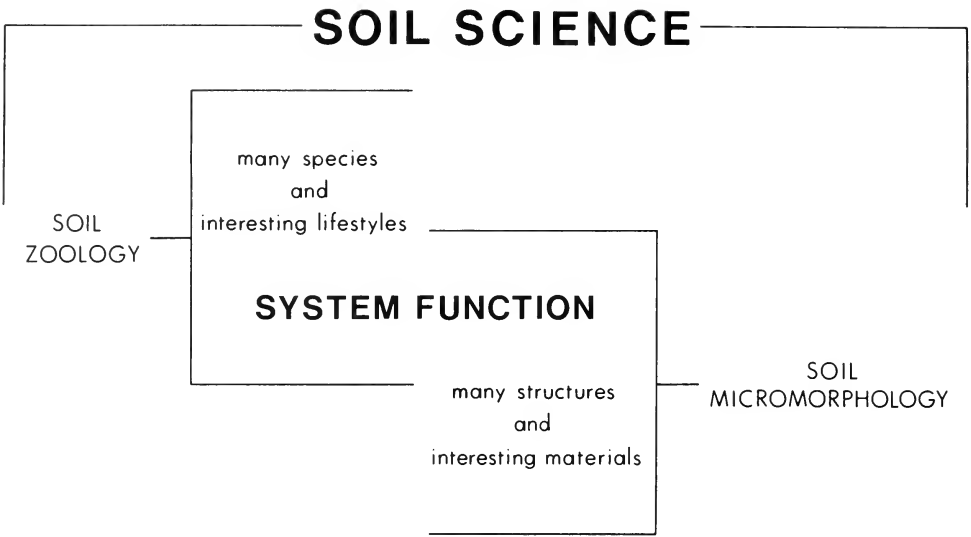


Fig. 1. Disciplinary interests showing overlap of soil micromorphology with soil zoology and the concept that the study of neither is complete without the other.

UNIFYING LINK

Systems consist of several components interacting with each other, and controlled by their environment. They are characterized by many cause-effect pathways and feedback processes, which give individuality to each system. Knowledge of that individuality is essential to structure man's interaction with ecological systems in a way that permits use of renewable natural resources that is stable in the long run. With respect to soil, it is clear that soils are being lost and degraded worldwide much faster than they are being generated and restored (Wolf, 1985).

As pointed out above, the unifying link between soil zoologists and pedologists which permits advancement of knowledge must be at a broader level of resolution than that required by either area of study alone. We argue that relationships between system function and system architecture provide that focus (Fig. 1).

For effective synthesis each part of the soil system merits detailed study and analysis in its own right. However, there are problems in each area which require information about the other. For example, while it is generally held that soil animals generate soil microstructures, it is not often clear which animals are responsible for a specific fabric or structure observed in thin sections of soil. In fact the relative impacts of soil organisms and abiotic processes are not well enough known to formulate general hypotheses. Similarly, habitable space and accessible substrates for various groups of soil animals cannot be evaluated without knowledge of soil pore size distribution and geometry relative to soil animal sizes and water film thicknesses needed to permit movement. Predator-prey interactions in soil are also controlled by pore size and geometry relative to organism sizes. Elliott *et al.* (1980) presented data consistent with the hypothesis that soil texture influences habitable pore space and hence trophic interactions in

terrestrial ecosystems. The above examples show how system function and architecture unite the two disciplines. The advancement of knowledge and practical benefits mentioned earlier are to be attained at this more holistic level.

CHALLENGES

Two challenges must be dealt with before progress may be made. The first is philosophical. Kevan illustrated how past concepts of soil animals have been shrouded in mythology. Ancient bestiaries portrayed themes of morality. Also, concepts of soils have varied from the mother of all life, to masses of ground rock, depending upon perspectives of the writer (Simonson, 1968). Soils have been associated with immortality and this has been passed to animals associated with them. Hill pointed out that the above metaphysical themes can be frequently found in discussions about man's use of soils or his interactions with it (see also Hyams, 1976).

Such a theme has important cultural consequences which are amenable to investigation within classics, anthropology, and sociology. However, it may lead to two different outcomes regarding objective examination of soils and soil animals. On one hand, it may generate a set of beliefs pertaining to function of soil systems and man's interaction with them which are not amenable to scientific scrutiny because they have not been derived from objective data. It may thereby hinder objective scientific examination of biophysical and biochemical interrelations between soil animals and the structure or function of the soils of which they are a part. On the other hand, stressing that roots of agricultural man extend from the soil can lead to a determined curiosity about how the system functions and how man can appropriately interact with and even become part of it. The challenge is to assure such objective analysis and synthesis.

The second challenge is mainly taxonomic. Soil animals are among the most abundant multicelled animals anywhere on earth (up to $10^6/\text{m}^2$) and their rates of reproduction and turnover can be startling. As pointed out by many authors in this proceedings, identification and classification of soil animals is both time consuming and difficult because of their small size, great diversity and relative obscurity among other members of the animal kingdom. For example, Greenslade estimated that 130,000 species of beetles in 11 families occur in soil. As documented by Fjellberg, Hoffman and Norton, the situation with respect to other groups of important soil arthropods is equally challenging and much more poorly known. However, few workers are engaged in soil animal taxonomy and, as Hoffman lamented, there is not much support for basic taxonomic work. Because research support is society's way of establishing value and prestige of workers, few young scholars are being attracted to these vital tasks (see also Crowson, 1970). As groups of animals are made accessible through production of taxonomic monographs, links between species and their environment or interactions within the system can be better explored. Edwards' presentation dealing with the effects of earthworms on soil structure and function illustrated what sort of advances are possible through experiments once a taxon is adequately known for ecological work. However, even with respect to composition of earthworm assemblages, we are relatively uninformed in North America. Similarly, soils contain innumerable fabrics with few researchers involved in their classification.

A proposal by Greenslade may partially resolve the zoological dilemma in the short run. He suggests that taxonomists be encouraged to reverse their usual procedures and start analysis by separating large groups of important soil animals into genera and species groups. Details of

species level classification can be worked out after a fauna is packaged for understanding by non-taxonomists. A first step in this important process is now underway. Dan Dindal is editing a general guide to soil zoology for North America which has been scheduled for publication by Wiley. Such treatments will be invaluable to soil biologists and should stimulate ecological work.

As noted by the Biological Survey of Canada (1982), a major impediment to development of soil ecology is a lack of taxonomic monographs and keys which are accessible to the non-specialist. Production of such material should receive high priority. As pointed out by Hoffman, the production of such basic descriptive taxonomic and faunistic work is often looked upon with disdain, even though it is most important for stimulating ecological work in the short run. Both Fjellberg and Rusek recognized need to distinguish ecological groups among taxa important in soils. Norton pointed out that study of phylogenetic relations is a major stimulus for classification and that such work has important benefits for synthetic studies. We do not argue that this approach should be abandoned. However, we submit that ecological interrelations can provide an alternative stimulus with different but complementary approaches.

Similarly, complexity of micromorphological classification of soils must be reduced and useful descriptions of microscale heterogeneity should be made available to non-specialists. The workshop session organized by McKeague and Fox provides direction for this effort. Again, synthetic work is appropriately focused by attention to the entire soil system (Fig. 2). Ultimately, this sort of work will be accomplished best by a new breed of scholar. We hope that the needs identified by this conference will be addressed by more flexible training of graduate students in soil ecology in the context of blended research programs that cross traditional departmental boundaries.

Studies of nutrient or energy flow through the soil system may be taken as an example of the above approach. Understanding energy flow requires, among other things, knowledge of where substrates are, where organisms are, and where they can go. A large proportion (40-80%) of soil pore space and surface area is inaccessible even to organisms of μm size (McGill, in preparation). Information is therefore required on physical and biological agents which reorganize soil fabrics to redistribute substrates and organisms. Such needs also link micromorphology, soil zoology and soil microbiology. The morphologist provides information on architecture, habitable spaces, and locations of substrates while soil biologists examine feeding habits and metabolism of various groups of organisms, their abilities to reorganize or produce specific fabrics, and to ingest mineral or organic material or both.

This conference has underscored the major advantages of joining the disciplines of soil zoology and pedology to foster growth of knowledge and understanding. Continued detailed analyses of each component are essential, but interactions among other components of the system can be an appropriate synthetic focus for study. We argue that the link between soil morphology and soil biology might best be described as soil biophysics. Thus, it includes but transcends faecal pellets.

SOME IDEAS

Microhabitats and Microcommunities

Although soils are viewed classically over the landscape at a macro scale of km^2 or m^2 many significant processes and mechanisms controlling them occur at a micro scale. Dindal showed that many distinct microenvironments exist in soil which lead to formation of distinct

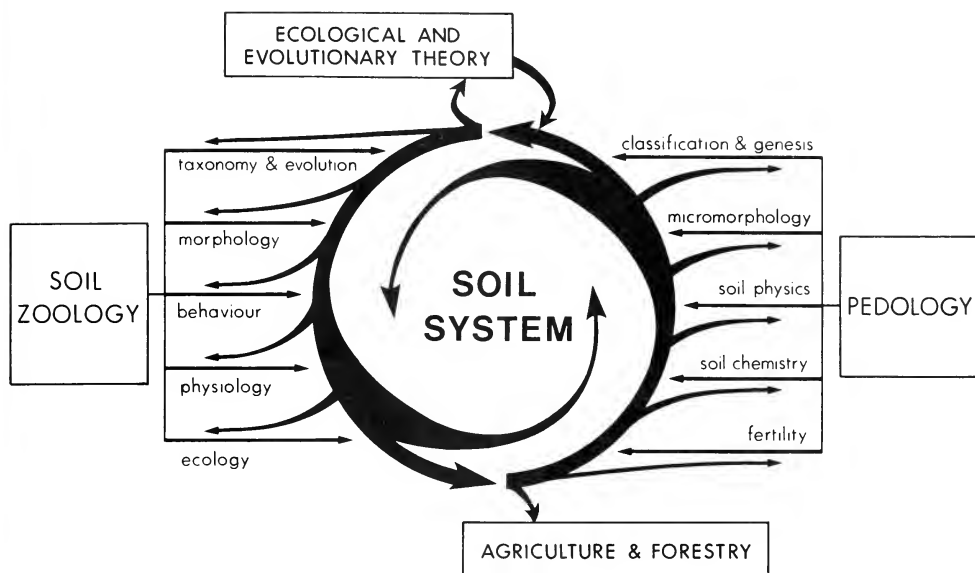


Fig. 2. Use of the soil system as a central focus for research. Work in the many subdisciplines of soil zoology and pedology can be synthesized in the dynamic framework of the soil system. The diagram emphasizes that spin-offs from synthesis will contribute to analysis in each subdiscipline. Spin-offs will also contribute to general theory and find applications in agriculture and forestry.

microcommunities and add to the spatial complexity of the macroenvironment. The soil system has tremendous spatial diversity which has been little studied in relation to its biological communities.

Implications of such microhabitat structure were cited by several authors. Greenslade estimated that only about 10,000 years are required for an area to be completely reworked by termites and Mermut showed the unique building block structures of such materials. Therefore, it is reasonable to deduce that much of the soil in tropical areas is composed of remnants of reworked termite mounds. Fjellberg mentioned that aggregation pheromones have been detected for Collembola and the resultant aggregations have obvious but unstudied implications for generation of microcommunities. Both Hill and Parkinson commented that soil animals are themselves microhabitats which move, influencing dispersal of smaller animals, bacteria and fungi. Water retained by surface tension around soil animals or their larval stages can be a significant proportion of the total water film space available to soil microorganisms (McGill, in preparation).

The guts of soil animals are also important microhabitats with respect to soil function. Parkinson mentioned that bacteria are unaffected or increase in numbers upon passage through the gut while fungi are damaged by passage through small organisms such as Collembola. The gut of earthworms is a moist microhabitat where substrates are in motion and new surfaces are acted upon by many smaller organisms. Fungal sporulation and spore movement are affected by soil pore size distribution.

A recurring theme of the conference has been the importance of faecal pellets as microhabitats which may dominate the fabric of some soils. Microcommunities and

microenvironments may be characterized as mixed culture systems. Three postulates flow from this concept: (i) species interactions such as symbiosis and, perhaps, mutualism may be more characteristic and important to soil communities than are the results of succession, (ii) soil animals not only alter their own environment, but are microhabitats for smaller organisms, and (iii) the environment of a soil organism, and hence controls of its activity, are a function of its size. Investigation of these three postulates could provide an initial framework for a more synthetic soil ecology.

Fabric Reorganization and Locational Control

Pawluk emphasized that the exact involvement of soil fauna in forming soil microstructures is inadequately understood for Canadian soils. A further problem, alluded to by Mermut, is the lack of agreement among micromorphologists about standardized interpretation of soil fine structure. Because Foster and Mermut, respectively, showed that soil animals can be involved in both breakdown of structural units and in homogenization of materials, a dynamic picture of soil micromorphology emerges. It appears that soil fabrics are in a constant state of slow change; being generated, broken down and reorganized in cycles over long times. Such fabric reorganization, when combined with the above ideas about microenvironment, lead to a concept of biotic flux among substrates and environments. Such alterations in environment and relocation of organisms near fresh substrates, or in barren locations could profoundly influence how the system functions. It also provides an additional link with soil microbiology, further emphasising the mixed culture aspect of the soil system.

The role of soil fauna in comminution of plant debris and in formation of the soil matrix is becoming better understood (Seastedt, 1984). Ideas about communities developed from studies of nutrient cycling can now be extended to include disintegration or comminution of soil microstructures. Further research into this aspect of relations between soil animals and soil structure is needed before the extent and significance of the process is known. Soil microstructure influences the local environment and probability of substrate-organism contact at microsites where biological processes occur. As a result, soil organic matter dynamics, and soil quality, are influenced by fabric reorganization which comprises both formation and comminution of microstructures. Soil animals may thereby provide an important control on soil organic matter dynamics and soil quality.

Associated with the above is the effect of location, within or on soil, on the activities and survival of organisms. For example Fjelberg pointed out the sensitivity of Collembola to water supply because of the absence of an exoskeleton. One strategy is to live within soil layers where relative humidity is higher. Other soil animals migrate up and down the profile in response to soil moisture changes. Altemüller showed that what an organism does in soil is influenced by its position, and so behavioural studies of soil fauna must take micromorphological diversity into account. At an even smaller scale, Foster showed how entrapment of organic molecules or bacterial cells can result in their persistence through protection from decomposition or lysis. The above locational control on organism function is fundamental to soil systems and appears in turn to be modified by fabric reorganization. A type of feedback is thereby generated because soil animals are among the agents responsible for fabric reorganization.

SUMMARY AND CONCLUSIONS

The structure and function of soil systems are interrelated. Feedback between microhabitat conditions and soil animals is characteristic of terrestrial ecosystems. The above interactions link soil micromorphology and soil biology. System function and soil biophysics therefore become the focus which permits advancement of knowledge in soil biology and pedology beyond the capabilities of either discipline in isolation. Reciprocity between soil fauna and other soil components must be recognized, however, and studied objectively before progress can be made.

Several ideas which may help guide future research have resulted from this synthesis. It is postulated that soil fauna regulate soil systems through trophic interactions and biophysical mechanisms. Trophic interactions which involve soil animals as microhabitats have been reemphasized. Symbiosis, mutualism, and cohabitation are characteristic of soil communities, perhaps superceding in importance interactions associated with successional changes. Biophysical issues relating to size and location appear important. The relevant microenvironment of an organism is clearly a function of its size. A related concept is that the location of an organism determines its behaviour and the dynamics of its populations. We propose that comminution and disintegration of microstructures be added to formation of microstructures and comminution of plant debris as a third biophysical mechanism by which fauna regulate soil systems. Faunal influences on the dynamic relationships between soil structure and function should receive major emphasis.

An immediate challenge remains to link specific groups of soil organisms to defined soil microstructures as seen in thin sections. Related to this challenge is our recommendation for a more ecologically useful approach to classifying both organisms and soil fabrics which is needed to permit such links to be developed.

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**ADDENDA: TECHNIQUES, EQUIPMENT, ADDITIONAL REFERENCES, AND
PRIORITIES FOR FUTURE STUDY**

SOIL MICROMORPHOLOGY

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ABSTRACT

Soil micromorphology is a tool for studying a part of the continuum, from landscapes to microvoids between soil particles. Methods are outlined for sampling soils and preparing thin sections for study under the microscope. Features such as voids, aggregates, coatings, mineral and organic particles and their arrangements are shown and described briefly. The potential is outlined for applications of soil micromorphology to studies of soil genesis and of the influence of fauna on soil properties. The annotated reference list aids interested readers to delve farther into the fascinating architecture of soil as viewed in thin sections rather than as amorphous dirt.

RÉSUMÉ

La micromorphologie des sols représente un outil permettant d'étudier une partie du continuum de la morphologie des sols, qui s'étend des paysages jusqu'aux espaces microscopiques entre les particules. Les auteurs exposent dans leur grandes lignes des méthodes pour échantillonner les sols et pour préparer des coupes fines pour étude au microscope. Ils montrent et décrivent brièvement certaines particularités des sols telles que des vides, des agrégats, des pellicules, des particules minérales et organiques et leurs arrangements. Ils discutent du potentiel qu'offrent diverses applications de la micromorphologie des sols dans l'étude de la genèse des sols et de l'influence de la faune sur les propriétés des sols. Une liste de références commentées aidera les lecteurs intéressés à se familiariser davantage avec le sujet fascinant de l'architecture des sols tels qu'observés en coupes minces, plutôt que comme amas de terre amorphe.

INTRODUCTION

Soil micromorphology is the sub-discipline of soil science that includes studies of the structure of relatively undisturbed soil samples with the aid of microscopes. It is part of continuum that begins with observations of the pattern of soils in the landscape, proceeds to studies of pedons (units of soil) representative of segments of that landscape, continues with description and sampling of horizons within those pedons, of aggregates within the horizons, and so on at increasing detail, to the study of features within aggregates as seen in thin sections with the microscope (Fig. 1). Soil features ranging in size from approximately 10 to 10,000 μm can be studied in this section with the polarizing microscope. Scanning electron microscopy (SEM) is applied to the study of smaller features (Bisdorn, 1981).

Micromorphological techniques were applied rarely in the study of soils prior to the publication of the book 'Micropedology' (Kubiena, 1938). The use of micromorphology

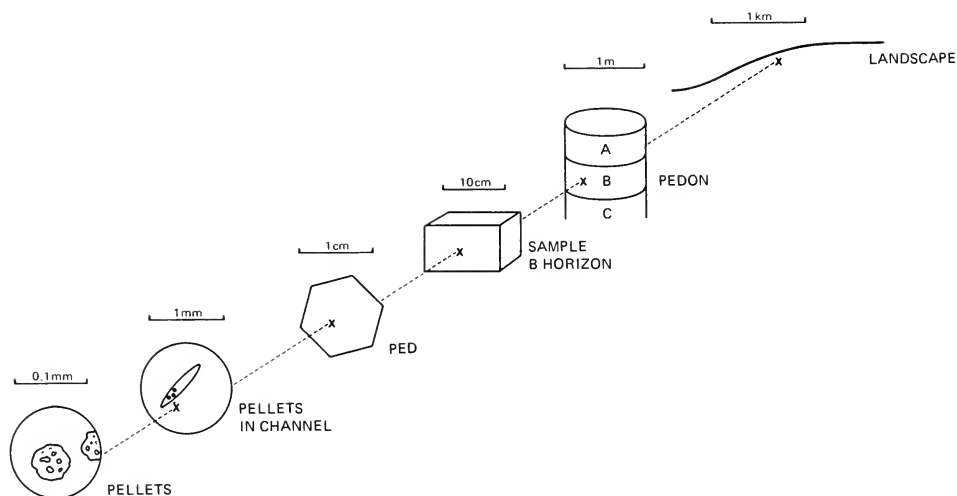


Fig. 1. Diagrammatic sketch indicating that soil micromorphology is a part of a continuum that includes macromorphology of soils in the landscape.

increased slowly until after the publication of Brewer's (1964) book "Fabric and Mineral Analysis of Soils". In it, Brewer defined terms precisely and outlined a system for describing soil microstructure; the book continues to be a basic reference. Currently, many soil scientists use micromorphological techniques in studies of soil genesis, physics, chemistry, minerals and living organisms. Only a few, however, specialize in micromorphology.

In this paper we outline the steps involved in sampling, in preparation of soil samples for study, and in applying micromorphological techniques to the study of soils. Examples are given of kinds of problems amenable to study by micromorphology; some involving soil fauna and related to soil structure are included. Further information on all aspects of soil micromorphology is included in the references listed.

SAMPLING

Sampling is a crucial step in micromorphology. The first step is to decide the purpose of the study. Suppose, for example, that the pedologist wants to determine the nature of the material that cements the sand grains in a cemented horizon of a sandy pedon. A single clod of the cemented material might be an adequate sample for preparation of a thin section, description by microscopy of the material that links the grains, and analysis of the material by energy dispersive X-ray analysis (Bisdorf, 1981). If, on the other hand, the purpose of a study is to determine differences in microstructure of surface horizons associated with differences in land use, a systematic sampling plan involving replication of samples of similar soils under different land use would be required.

After establishing the purpose and deciding on the sampling plan, the next step is to collect the samples. The fundamental requirement is to obtain samples without altering the soil fabric, the arrangement of particles and voids. For unconsolidated mineral soil materials, this is usually done by pushing a metal frame or an open metal box, a Kubiena box, into the horizon to

be sampled. Boxes of different sizes are used depending on habits, purpose of the study, and nature of the soil. We use metal frames 8 x 6 x 5 cm, 8 x 6 x 2.5 cm and 6 x 4 x 2.5 cm made from 20 gauge galvanized iron with the largest faces, 6 x 8 or 6 x 4 cm, open. The frame may be pushed by hand or preferably jacked into a vertical or horizontal exposure of the horizon of interest. The sample is trimmed flush with the edges of the frame, and its orientation is marked on the metal frame. The trimmed sample is placed in a plastic bag to avoid loss of water, and the open faces are covered with 9 x 7 cm pieces of plywood which are taped securely in place. The site number and sample depth are marked on the sample with waterproof ink. Information on the site and the sample is recorded in either a notebook, or a form such as a CanSIS file form for soil data (Day, ed. 1982).

If the horizon to be sampled is strongly coherent, such as a cemented horizon, a clod may be broken out, placed in a plastic bag, taped and labelled as indicated. Organic soil samples such as peat may be obtained with a Macaulay sampler, which provides half a cylindrical sample approximately 3.5 cm in diameter. These samples are placed in half cylinders of 3.75 cm PVC piping, enclosed in a plastic bag, protected with a wooden cover, taped and labelled. Further information on sampling is available (Sheldrick, 1984).

PREPARING SAMPLES FOR MICROMORPHOLOGICAL STUDY

Stereomicroscope

For some purposes such as describing the shapes and sizes of aggregates smaller than 2 mm, it is useful to examine samples under a stereomicroscope at magnifications of 5 to 30x. Such data complement macromorphological information obtained in the field.

Impregnating Samples for Preparation of Thin Sections

Most soil materials are unconsolidated so it is necessary to consolidate them by filling the pores with plastic and hardening before preparing thin (20 or 30 μm) sections. Water must be removed prior to impregnating the soil with most of the plastics that are used. Three methods have been used for removing water (Murphy, 1983): (1) oven drying - this results in shrinkage of many soil materials and hence alteration of pore sizes, (2) freeze drying - this results in ice crystal formation within the sample and, hence, some disruption of the fabric, (3) exchange of water by acetone - this results in some dissolution of organic components but it is the best of the three methods for preserving the soil fabric. Details of the drying procedures are given by Fitzpatrick (1984), Sheldrick (1984) and references cited therein.

After water is removed by oven - or freeze-drying, the sample is put under vacuum so as to remove air from voids, and the plastic mixture is added under vacuum. For acetone-exchanged samples, voids are filled with acetone so vacuum is not necessary during the addition of plastic. A variety of polyester resins diluted with thinners such as acetone, or epoxy resins, are used (see Jongerius and Heintzberger, 1975; Sheldrick, 1984; Fitzpatrick, 1984). Catalysts may be added to increase the rate of polymerization and fluorescent dyes may be added to facilitate study of pores. We use a polyester resin - acetone mixture; Uvitex OB (Ciba-Geigy), a compound that fluoresces in ultraviolet light, is added in some studies (Sheldrick, 1984). Usually in our laboratory 2 weeks to 2 months are required from the time the resin is added until the impregnated block is hard. For some purposes, it is appropriate to use a resin mixture that hardens in a few hours. Final curing of the plastic is done by heating the block to 60°C.

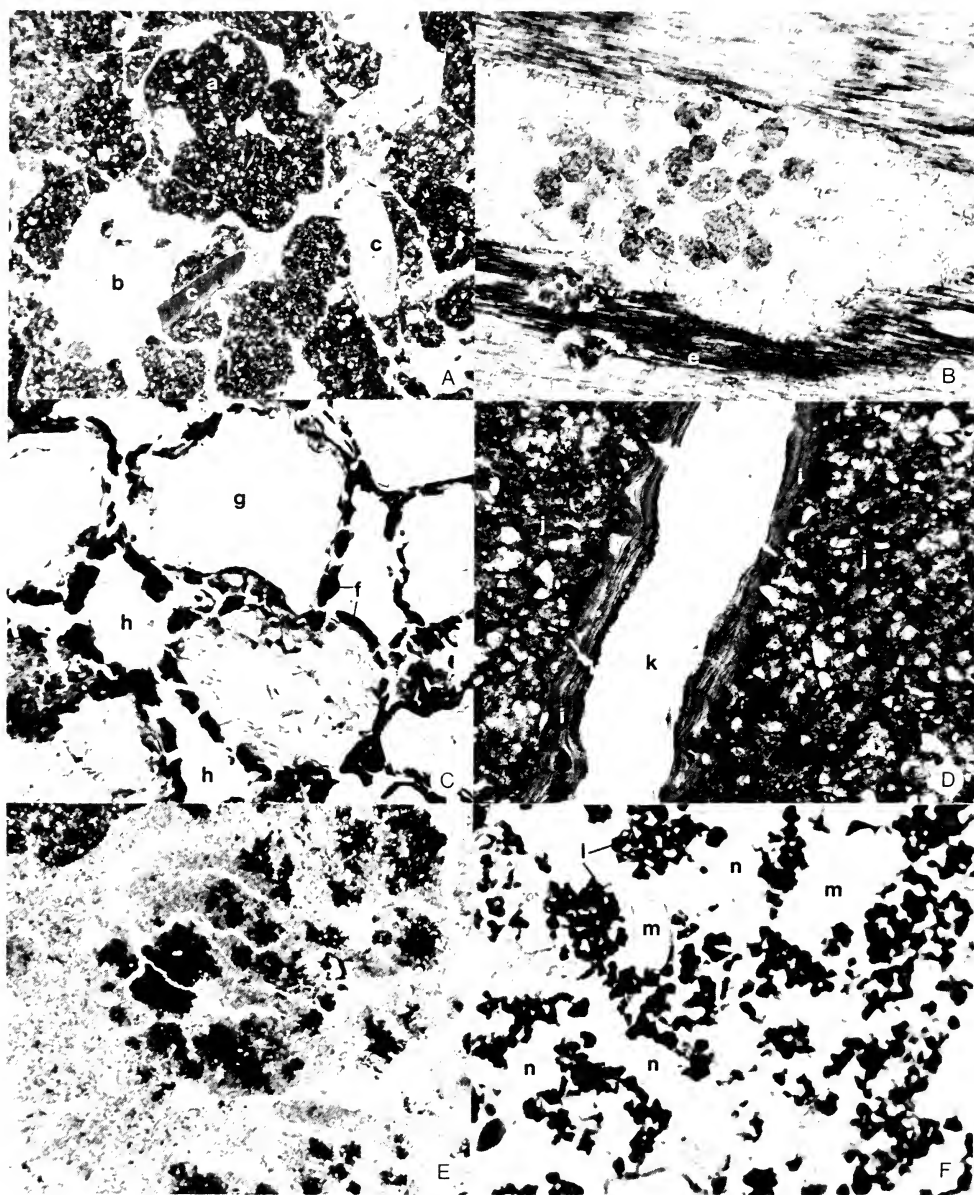


Fig. 2. Photomicrographs of features in soil thin sections. A. Partly-fused, rounded aggregate 'a' due to earthworms, a large void 'b' and organic fragment 'c' in the Ah horizon of a clayey Humic Gleysol near Ottawa. The width of the field is 8 mm. B. Fecal pellets 'd' of mites in decaying wood tissue 'e' from an Om horizon of an organic soil in Ontario. The width of the field is 1.3 mm. C. Dark reddish-brown, amorphous coatings 'f' on sand grains 'g', and packing voids 'h' in the Bhc horizon of an Ortstein Humic Podzol from New Brunswick. The width of the field is 1.3 mm. D. Clay coating 'i' on surfaces of dense clayey peds with embedded silt and sand grains 'j' and a planar void 'k' in the Bt horizon of an Orthic Gray Luvisol from Ontario. The width of the field is 1.3 mm. E. Reddish-brown and black nodules enriched in Fe or Mn, of Fe and Mn in the Bg horizon of an Orthic Humic Gleysol from the Fraser Valley, British Columbia. The field is 3.9 mm wide. F. Dark reddish-brown aggregates 'l' in spaces between sand grains 'm' in a porous 'n' Bf horizon on an Orthic Humo-Ferric Podzol from Québec. The width of the field is 1.3 mm.

Preparing Thin Sections

The hardened sample is cut with a diamond saw to obtain a horizontally or vertically oriented slab depending on requirements, approximately 1 cm thick. For samples containing Uvitex OB, the cut face of the block may be photographed under ultraviolet light to show the pore pattern. Pore configuration may be characterized quantitatively using an image analyzer (Murphy, 1982; Bullock and Murphy, 1983). The sample orientation and number is marked on the slab and the area to be used for thin sections is selected. The dimensions of the thin section may be as large as the block or approximately 2 x 3 cm depending on the equipment available and the purpose of the work. A chip of the appropriate size is cut, its orientation is marked, one side is ground smooth on a diamond lap and cleaned. The chip is warmed on a hot plate, epoxy cement is applied and a glass slide is fixed to the chip. The mounted chip is cut to a thickness of approximately 0.5 mm on a diamond saw. It is ground on diamond laps with progressively finer grit to a thickness of 20 to 30 μm . The thickness is checked by observing the section under crossed polarizers with a polarizing microscope. Quartz grains appear white to grey if the thickness is correct. The section is cleaned, a cover glass is applied with epoxy, and the sample orientation and number are marked on the microscope slide.

Describing Thin Sections

Systems for describing thin sections are outlined in several publications (Brewer, 1964; FitzPatrick, 1984; Bullock *et al.*, 1985). We refer to the last system as it was developed by an international committee. Sections are described under the following headings:

Microstructure.— The size, shape and arrangement of particles and voids. For example, note the rounded aggregates, large voids and organic fragments in an Ah horizon (Fig. 2A).

Mineral and Organic components.— Mineral grains larger than approximately 20 μm can be identified by skilled microscopists. The nature and degree of decomposition of organic components may be identified. For example Fig. 2B shows a decaying woody root fragment with a cluster of mite pellets.

Groundmass.— The proportions and arrangements of coarse and fine components. In some samples, the fine material occurs as coatings on coarse grains (Fig. 2C); in others coarse grains are imbedded in a fine matrix (Fig. 2D).

Pedofeatures.— Features of the fabric due to soil genesis. For example, the coating of clay on the heterogeneous matrix material adjacent to the planar void (Fig. 2D) is a pedofeature due to deposition of clay from suspension. The dark brown and black nodules (Fig. 2E) are pedofeatures due to segregation of Fe and Mn oxides in a soil that is saturated and under reducing conditions periodically. The microaggregates in the B horizon of a Podzolic soil may be due to physical processes or to soil fauna (Fig. 2F).

APPLICATIONS OF SOIL MICROMORPHOLOGY

Soil micromorphology has been applied principally to studies of soil genesis. In recent years, however, applications to other areas of soil science, including soil zoology, have increased markedly. Some examples of these applications are discussed briefly; others are found in Bullock and Murphy (1983) and in proceedings of previous meetings of the International Working Meeting on Soil Micromorphology.

Among the major applications of soil micromorphology in studies of soil genesis is seeking direct evidence of translocation of fine particules from near-surface to subsurface horizons (see

papers in Bullock and Murphy, 1983; and Douglas, 1985). Surfaces of peds in horizons from which clay has been removed are commonly uncoated or they may have coatings of coarser grains due to loss of clay. Horizons in which clay has been deposited commonly have surfaces of peds coated with oriented clay which appears finer and more uniform than the matrix material (Fig. 2D). Micromorphology has been applied also in many studies of podzols, especially their B horizons in which amorphous organic Fe, Al materials accumulate as coatings (Fig. 1C), as aggregates between grains (Fig. 2F), or both. A controversy continues over the origin of the aggregates (Fig. 2F). Some believe that they are fecal pellets; others believe that they are the result of physical processes, especially shrinkage on drying of the gel-like amorphous materials.

Micromorphology may be applied to soils studies other than those focused on genesis; a few examples are listed. Micromorphological and associated sub-microscopic techniques are powerful tools for studying the weathering of minerals in soils (Bisdorf, 1981). Attempts have been made to relate the sizes and shapes of voids seen in thin section to water flow in soils (Bouma *et al.*, 1979), Babel (1975) has shown the potential of micromorphological techniques in studying, at high magnification, the decomposition of organic materials. Fox (1984) outlined a system for describing the complexity of organic materials at a wide range of magnifications. Other examples are given in proceedings of this symposium.

Kubiens (1938) was ahead of his time in recognizing the influence of soil fauna on structure and he observed soil fauna directly in the field. Bal (1982) reviewed the literature on the subject and reported results of his experiments showing faunal effects on soil structure. The growing awareness in North America of the role of soil fauna will be accelerated by this symposium. Many questions regarding the origin of aggregates and tubules in soils remain to be resolved and caution will be required to avoid overstating the roles of soil fauna. Hypotheses that could account for the common presence of rounded aggregates ranging in size from approximately 20 μm to several mm must be tested objectively for different soil horizons. Micromorphology will be a useful tool in such studies.

CONCLUSION

Examination of thin sections with the microscope complemented by submicroscopic techniques leaves the observer with an expanded appreciation of the organized heterogeneity of soil horizons. Soil samples prepared for chemical analysis appear to be amorphous dust. Thin sections show the complex architecture of a host of different mineral crystals, aggregates of fine particles, amorphous components and voids of differing sizes and shapes, some of them made by soil fauna. Having viewed soil in thin section, the observer incorporates into his model of soil the concept of its complex architecture and appreciates the influence of biological forces on that architecture.

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**PRIORITIES FOR THE INTEGRATED DEVELOPMENT OF SOIL
MICROMORPHOLOGY AND SOIL ZOOLOGY: RESULTS OF A BRAINSTORMING
SESSION**

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During a two-hour workshop, 50 soil micromorphologists and soil zoologists participated in an exercise designed to identify priorities for the integrated development of their disciplines.

Several months before this workshop, a list of 20 needs of soil zoologists, identified by us, was circulated to other speakers as background materials to the workshop. This list was also included in the registration package given to all symposium participants. These topics have been integrated into the full list of identified needs given below (those not mentioned during the workshop have an asterisk).

The participants were divided into 10 groups of five, each group including representatives of both disciplines. Two five minute exercises were then conducted during which participants brainstormed (listed, uncritically, as many things as they could think of in the time available) on the questions "in what ways can members of the other discipline benefit your discipline" and "in what ways can members of your discipline help the other discipline". One member from each group recorded responses, and all responses were then listed on flip charts and posted in view of all participants.

Groups were then encouraged to expand their initial lists by imagining that there were no restraints on their proposals and that ideal conditions prevailed. Finally, each group was asked to identify, taking into account their previous suggestions, the three most important needs to achieve the integrated development of the disciplines. These priority needs were combined and then arranged under the following six headings. The more extensive list of suggestions, referred to earlier, is given in an Appendix using the same headings.

PRIORITY NEEDS

1. Policy

- Identify changes in government policies that will facilitate the integrated development of soil micromorphology and soil zoology.
- Identify ways to translate research findings into improved soil management practices.
- Improve public education (use of media, *etc.*) concerning the importance of these disciplines.
- Increase the number of university positions in these disciplines.
- Establish multidisciplinary "Soil Institutes" (building, for example, on the experiences of Dr. Josef Rusek, Director of the Laboratory of Soil Biology, Institute of Landscape Ecology, Czechoslovakia).

2. Research

- Facilitate and support multidisciplinary research (from planning to publication).
- Improve international planning and cooperation of research programs (building on International Biological Program experience).

3. Education

- Establish educational programs that integrate these disciplines, at least at the University level.
- Provide general and specialized short courses (and field trips), covering the various aspects of these disciplines.

4. Networking

- Produce a directory of specialists noting their fields of interest and current projects.
- Continue to hold joint symposia for these (and other related) disciplines.

5. Literature

- Produce low cost, high quality textbooks providing syntheses of what is known and unknown in these disciplines.
- Prepare illustrated, comprehensive, easy-to-use keys and atlases of soils and soil organisms.

6. Techniques

- Develop reliable, standardized, inexpensive and easy-to-use techniques for conducting research in these disciplines.

APPENDIX: FULL LIST OF NEEDS IDENTIFIED DURING WORKSHOP

1. Policy

- Dissolve disciplines (at least at the edges).
- Shift emphasis to long-term multidisciplinary studies.
- Identify potential sources of institutional support.

- Promote institutional support.
- Improve public education (better use of media *etc.*).
- Establish chairs in soil biology/soil micromorphology.
- Establish "Soil Institutes" integrating these and other related disciplines.
- Facilitate interaction between members of these disciplines in universities, institutes, *etc.*.

4. Networking

- Establish a common journal.
- Produce a directory of specialists noting their fields of interest and current projects (including willingness to identify and describe soils and soil fauna).
- Establish data banks with minimum access costs.
- Continue to hold joint symposia for these (and other related) disciplines, including workshops and think-tanks *e.g.*, to continue the initiative described in this paper.
- * Prepare directories of special facilities and equipment that are not widely available.

2. Research

A. Requests from soil micromorphologists to soil zoologists:

- Clarify relationships between soil community and soil type.
- Identify and provide information concerning the distribution (horizontal and vertical) of soil animals, exuviae and faeces.
- Clarify the ecological importance and influence on physical factors of different species/genera/orders of soil animals, *e.g.*, their role in decomposition of organic matter.
- Provide qualitative and quantitative data concerning the feeding habits of different soil animals.
- Describe the niche characteristics of different soil animals.
- Collaborate in research projects (from planning to publication) and establish multidisciplinary research teams.
- Consider the needs of soil micromorphologists when selecting soil zoology research topics.
- Provide physico-chemico-biological descriptions of faeces of different soil animals.
- Describe the major 'types' of soil communities.

B. Requests from soil zoologists to soil micromorphologists:

- Describe the major chemical transformations in soil.
- Describe the micromorphology of different soils, including identification of potential food sources, mineral and humus composition, pore spaces, *etc.*
- Describe the micromorphology of the stages in humification.
- Collaborate in research on "problem soil profiles".
- Collaborate in research on the acceleration of soil-forming processes.
- Describe the impact of salinization on soil structure and function.

6. Techniques

- Develop non-destructive research techniques (*e.g.*, sampling).
- Develop reliable, standardized, inexpensive and easy-to-use research techniques.
- Develop improved methods for embedding, staining, making thin sections and analyzing soil (*e.g.*, discover a water miscible, non-toxic embedding resin).
- * Prepare “Cookbooks” of techniques (including hints not usually given in textbooks).
- * Prepare a “Consumer guide” to equipment (giving advantages and disadvantages).
- * Prepare a “Cookbook” of statistical techniques and a list of computer and micro computer program packages that are especially useful for soil fauna and soil micromorphology research.

3. Education

- Emphasize to soil scientists the living reality of soil.
- Share information “at the microscope” (soil fauna/faeces identification, ped description, *etc.*)
- Organize joint field trips.
- Provide general and specialized short courses (including laboratory experience and field trips) covering the various aspects of these disciplines (for professionals and non-professionals).
- Guide students enrolled in each of the disciplines to attend one or more courses in the other discipline.
- * Produce learning packages, tapes, films, slide sets, video-tapes, modules *etc.*, on all aspects of these and related disciplines, and prepare guides to existing materials.

5. Literature

- Prepare guides (annotated bibliographies, *etc.*) to the basic literature.
- Prepare illustrated, comprehensive, easy-to-use keys to adult and immature soil animals (by habitat, region, feeding group, *etc.*).
- Produce low-cost, high quality textbooks.
- Prepare basic comprehensive atlases of soil micromorphology (including three dimensional views of pore spaces).
- * Prepare thesauri of soil zoology and soil micromorphology.
- * Prepare comprehensive dictionaries of soil zoology and soil micromorphology.
- * Produce directories of translations of relevant books and papers.
- * Produce directories of grants, with tips on grantsmanship.

A VARIATION OF THE MERCHANT-CROSSLEY SOIL MICROARTHROPOD EXTRACTOR

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The Merchant-Crossley extractor is an inexpensive apparatus which rivals more elaborate constructions in efficiency (Merchant and Crossley, 1970; Seastedt and Crossley, 1978). The design suggested here involved modifications to improve ease of operation and to minimize lateral contaminations. As in the original, the 2 inch diameter soil corer used is commercially available from "Art's Machine Shop" (Harrison and Oregon Trail, American Falls, Idaho 83211) and costs slightly more than \$100 (U.S.). The steel sampling cup can be ordered to any length, as can the aluminum retaining cylinders.

Soil cores taken in the field are trimmed at the bottom end, placed in individual plastic bags, left open at the top, and kept in an ice-chest until extraction. The top of each retaining cylinder, with the core intact, is covered with a small individual fiberglass screen. It is cut slightly larger than the cylinder and held in place by a plastic retaining-cylinder cover (also available from "Art"), from which most of the center has been cut out so that little more than a "lip" is left to hold the screen in place. This soil-cylinder-screen unit is then inverted, placed into the extractor hole from below, and held up by two heavy rubber bands, wrapped around the upper part of the cylinder.

The extractor itself is constructed from varnished 1/2" plywood. I have found the most convenient design to be that shown in the accompanying figure. Heat is provided by 7 watt "nite-lite" bulbs, either used in a Christmas tree string, or preferably individually wired "cleat receptacles" attached to the extractor cover. Individual tin or aluminum (12 oz.) cans (with both ends cut out) between the top and core provide reflection and maintain heat. Due to the individual nature of each unit, there is no "edge-effect" in terms of extraction efficiency, as there often is with extractors using a common heat source. Because of the low wattage of each 20-unit extractor, an inexpensive household dimmer-switch can be wired and attached to the outside of the cover for the control of light intensity.

The extractor is very adaptable in terms of collection method. As in the original version, collection into alcohol can be accomplished with the use of powder funnels forced through holes cut into caps of collecting vials. Vials are about 1/3 filled, so that room is left for the funnel which is rinsed with alcohol after extraction is complete.

If extraction over water is preferred, appropriate size plastic jars are used instead of the powder funnel-vial unit. An ideal, inexpensive screw-cap plastic jar is a 4 1/2 oz. wide-mouth specimen-container used in hospitals (Superior Plastic Products Corp., P.O. Box 2128, Providence, RI 02905). The cap (with the center cut out to the diameter of the cylinder cap) is attached to the underside of the middle layer of the extractor, so that the jar (1/3 filled with water) can be screwed in from below. An effective, and very inexpensive canister extractor is

the result. It prevents drying of the core from below, and eliminates the use of funnels, which provide condensation surfaces and allow potential escape. Seastedt and Crossley (1978) had somewhat poorer results with a canister-style apparatus, but this was probably due to their use of alcohol, instead of water, as a collecting fluid.

The compact 20-unit extractors can be removably wall-mounted, shelf-mounted, or placed on small tables; they can even be stacked if side ventilation holes are provided. They can be used in refrigerators or both small and large environmental chambers and are extremely portable.

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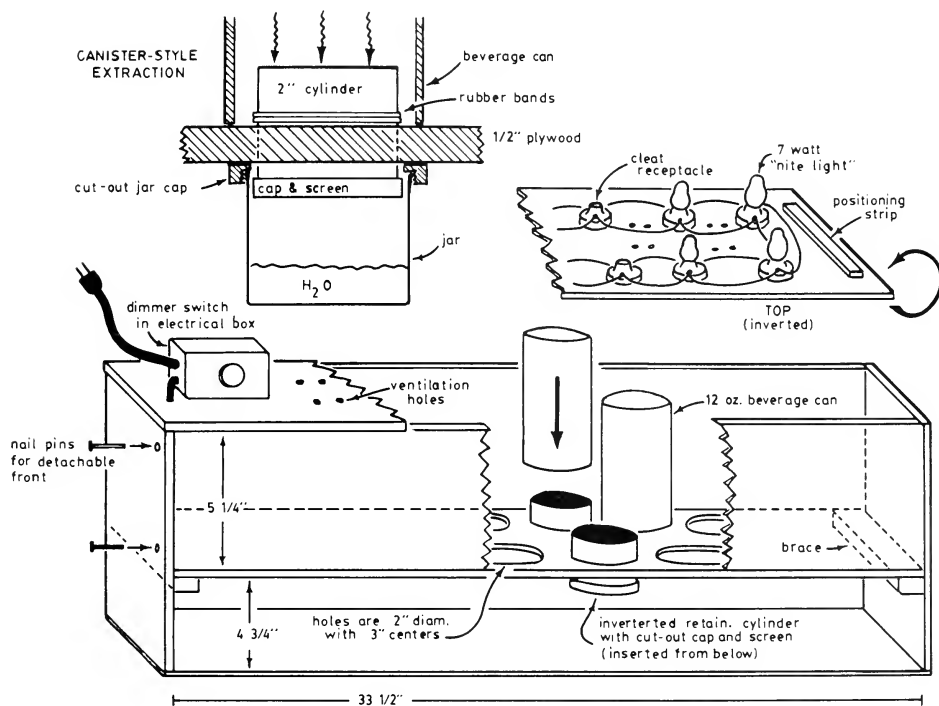


Fig. 1. Diagram of a Modified Merchant-Crossley Extractor for Soil Microarthropods.

SUPERIOR MICRO-NEEDLES FOR MANIPULATING AND DISSECTING SOIL INVERTEBRATES

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Sturdy, yet very sharp, needles for dissecting microarthropods or manipulating small objects cannot be purchased, but can be easily made with little equipment. The standard use of insect minuten-pins is often not satisfactory due to poor quality control, improper taper, flaking and corrosion and other problems which can be avoided by electrolytically produced needles.

A suggested apparatus is shown in the accompanying figure. A deep well slide is attached to the bottom of a standard petri-dish with a strong epoxy cement (the top covers the apparatus when not in use). Then an old microscope stage slip (or a similarly shaped piece of thin aluminum sheeting) is epoxied to the slide, with the bent tip pointing into the well (touching the bottom, if possible) and the other end bent upwards about 1/2 inch. Cover the clip with epoxy, except at the bent ends.

The needle is cut from 10 mil (0.25 mm) tungsten wire, and held in a zero-closure pin-holder. Wire can be obtained, for example, from Alfa Products, Thiokol/Ventron Division, 152 Andover Street, Danvers, MA 01923 (catalogue #0371) and costs about \$20 (U.S.) for a 20 m roll (a life-time supply). The pin-holders can be obtained from Fine Science Tools Inc., 321-B Mountain Highway, North Vancouver, B.C. V7J 2K7 and cost \$8-10 (U.S.) each depending on style and length. Good holders are recommended, rather than cheaper varieties which are not zero-closure.

The only other necessary equipment is a D.C. power supply, about 5-10 volts and 0.5-1.0 amp. Some calculator-style supplies are satisfactory, but a transformer from an old stereo-microscope or compound microscope illuminator would be ideal. Also, the output leads from the transformer need to be supplied with electrical attachment clips for good contact.

In operation, one fills the well with 10% KOH, attaches one lead to the clip of the well slide and the other to the end of the pin-holder (with the appropriate length of wire in place). Correct polarity is essential, but usually has to be determined the first time by trial and error (if the wire does not sharpen after a half minute or so, switch leads). Once the transformer is activated and the needle is placed in the KOH, rapid bubbling should surround the needle. Rate of electrolysis is controlled by the transformer setting and the distance the needle is held from the well-slide clip. A good simple needle can be made in less than one minute.

The desired taper of the needle is a function of its projected use and individual preference. Taper can be controlled by the angle at which the needle is immersed in the KOH bath.

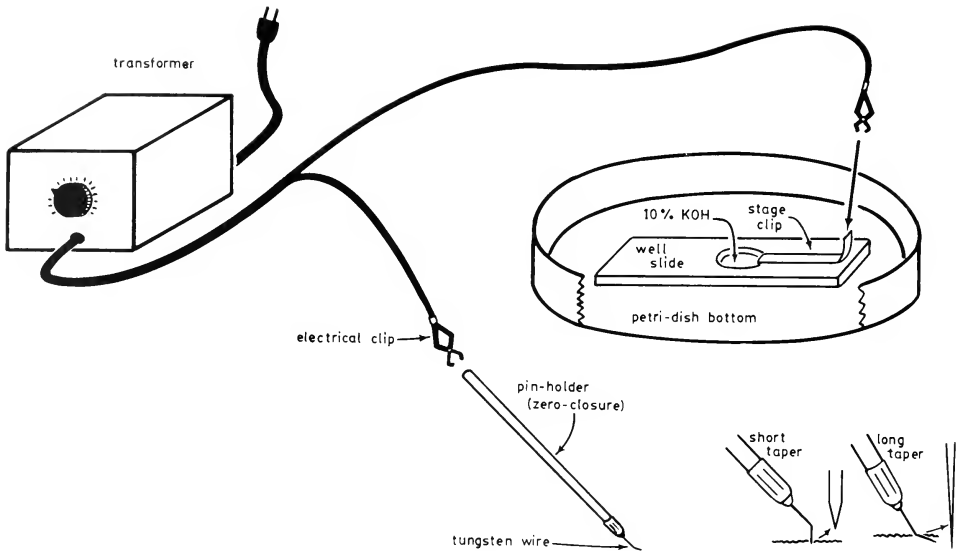


Fig. 1. Diagram of Equipment and Procedure for Manufacture of Micro-Needles used in Morphological Dissection of Soil Invertebrates.

Near-vertical orientation produces a short, thick taper; near horizontal orientation produces a long, fine taper. The tip will be destroyed if accidentally touched to the well-slide clip while current is on.

Bending the needle with forceps prior to electrolysis is usually desirable for working comfort. Micro-hooks can be first bent, then electrolyzed; another way is to first taper a needle in the usual way and then press it against a hard object to curl it, with finishing touches put on after that.

Electrolysis causes a mist of KOH to be produced, so a good place to work is in a fume-hood. Have a nearby stereo-microscope set up to intermittently check progress, but do not operate too close to the microscope. Once formed, needles can be redressed in a few seconds and the tungsten wire need be replaced (or re-bent) only after repeated quick sharpenings. Since the tips are very fine, cover the end of the pin-holder when not in use. The cut-off tips of soft plastic disposable eye-droppers serve nicely, as do some of the stiffer rubber bulbs, or tubings.

SOIL INVERTEBRATES: MAJOR REFERENCE TEXTS

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This bibliography is incomplete but should serve as an introduction to the literature on the various groups of soil invertebrates. (Research papers are almost all omitted. Works in languages other than English (some of which fill important gaps) are almost all omitted; references to most of them will be found in the books listed.

GENERAL

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Organismes du sol et production primaire. IV Colloquium Pédobiologiae. Institut National de la Recherche Agronomique, Paris. 590 pp.

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Anderson, J.M. and A. MacFadyen. (Editors). 1976. The Role of Terrestrial and Aquatic Organisms in Decomposition Processes. Blackwell, Oxford, England. 474 pp.

Proceedings of British Ecological Society Symposium. Covers physico-chemical aspects of the environment, interrelationships of organisms involved and their role in soil and fresh water ecosystems and modelling of decomposer systems. Refs. after each paper.

Bornebusch, C.H. 1930. The Fauna of Forest Soil. Nielsen & Lydiche, Copenhagen. (From Forst. Forsogsv. i Danmark, II: English and Danish). 224 pp.

A classic.

Brauns, S. 1968. Praktische Bodenbiologie. Gustav Fisher Verlag, Stuttgart. xviii + 470 pp.

Classic text on Soil Biology with a practical emphasis. Not as yet translated into English.

Refs. after each chapter.

Burges, A. and F. Raw. (Editors). 1967. Soil Biology. Academic Press, New York. 532 pp.

An anthology of technical papers discussing biology of different classes of soil life.

Cloudsley-Thompson, J.L. 1958. Spiders, Scorpions, Centipedes and Mites. Pergamon Press, Oxford. 278 pp.

(Paperback edition 1968). Includes most groups other than hexapods besides those in title.

Illustrates their diversity and versatility. Refs. after each chapter.

Cloudsley-Thompson, J.L. 1967. Microecology. (Institute of Biology's Studies in Biology, 6).

Edward Arnold Ltd., London. 48 pp.

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⁵Research Centre, Agriculture Canada, London, Ont., N6A 5B7.

Simple introduction to predominantly soil and related fauna. 23 refs.

Cloudsley-Thompson, J.L. & J. Sankey. 1961. Land Invertebrates. Methuen, London. 156 pp.

Introductory, relates to various groups of soil animals.

Coinneau, Y. 1974. Introduction a l'étude des Microarthropodes du sol et de ses annexes.

Documents pour l'enseignement pratique de l'écologie. Doin, Paris, 188 pp.

Excellent textbook, with chapters on abiotic and biotic factors in the soil, techniques, taxonomy and biology and a comparison of the microfauna of different soil types.

Danks, H.V. 1979. Canada and its insect fauna. Mem. Ent. Soc. Can. 108: 573 pp.

Synopsis of information available on insects and related arthropods in Canada.

Dickinson, C.H. and G.J.F. Pugh. (Editors). 1974. Biology of Plant Litter Decomposition. Vol. 1 & 2. Academic Press, New York. 241 & 775 pp.

The most comprehensive work on the subject. Refs. after each chapter.

Dindal, D.L. (Editor). 1980. Soil Biology as Related to Land Use Practices. Proc. VII Int. Soil Zoology Colloquium. Office of Pesticide and Toxic Substances, EPA, Washington, DC. 880 pp.

Current research on the effects of human ameliorations and perturbations on soil organisms.

Doeksen, J. and J. van der Drift. (Editors). 1963. Soil Organisms. North Holland Publ. Co., Amsterdam. 453 pp.

Research on the biology and ecology of soil organisms. Refs. after each chapter.

Drift, J. van der. 1951. Analysis of the Animal Community in a Beech Forest Floor. Institut v. Toegepast Biologisch Onderzoek in de Natuur, Mariendaal, Oosterbeek, Netherlands. [From *Tijdschr. v. Ent.* 94 (1)]. 168 pp.

Oligochaetes and molluscs receive brief notice.

Graff, O. and J.E. Satchell. 1967. Progress in Soil Biology. North Holland Publ. Co., Amsterdam. 656 pp.

Anthology of technical and specialized papers from German colloquium. Half of papers are in German. Refs. after each presentation.

Haarlov, N. 1960. Microarthropods from Danish Soils: Ecology, Phenology. Andelsbogtrykkeriet, Odense, Denmark. (From *Oikos*, *Suppl.* 3). 176 pp.

Jackson, R.M. and F. Raw. 1966. Life in the Soil. Edward Arnold Ltd., London. 60 pp.

Authors from Rothamsted discuss soil ecology and ways of studying it. 21 refs.

Kaestner, A. 1967. Invertebrate Zoology. Vol. I. John Wiley and Sons Inc. 597 pp. (Translation of earlier German work).

Includes information on biology, ecology and general classification of platyhelminths, rotifers, nematodes, molluscs and annelids.

Kaestner, A. 1968. Invertebrate Zoology. Vol. II. John Wiley and Sons Inc. 472 pp. (Translation of earlier German work).

Includes information on biology, ecology and general classification of tardigrades, arachnids, centipedes, millipedes, pauropods and symphylans.

Kaestner, A. 1970. Invertebrate Zoology. Vol. III. John Wiley and Sons Inc. 597 pp. (Translation of earlier German work).

Includes information on biology, ecology and general classification of isopods and amphipods.

Kevan, D.K.McE. (Editor). 1955. Soil Zoology. Butterworths Scientific Publications, London & Academic Press, New York. 512 pp.

First integrated study of soil fauna on an international footing. It is still a basic reference

work. Refs. after each paper.

Kevan, D.K.McE. (Editor). 1968. *Soil Animals*. H., F. & G. Witherby, London, & Philosophical Library Inc., New York. 244 pp.

Corrected and slightly augmented reprinting of 1962 edition which covers all groups of soil animals.

Kuhnelt, W. 1976. *Soil Biology: with special reference to the Animal Kingdom*. 3rd ed. Faber & Faber, London. 397 pp.

Draws mostly on work from European soils, but is still very good for general description of soils and the animals in them. 1700 refs.

Lawrence, R.F. 1953. *The Biology of the Cryptic Fauna of Forests*. A. A. Belkema, Cape Town. 408 pp.

Emphasis on fauna of indigenous forests of South Africa. 13 pp. of refs.

Lebrun, Ph., H.M. André, A. de Medts, C. Gregoire-Wibo and G. Wauthy. (Editors). 1983. *New Trends in Soil Biology*, Proc. VIII. Intl. Colloquium of Soil Zoology, Louvain-la-Neuve, Belgium. 1982. 700 pp.

Most recent text on research in soil biology. Topics are covered in four major areas: the role played by soil fauna in mineral cycling; functional relationships between soil organisms; ecophysiology of soil animals and restoration capacity of soil communities.

MacFadyen, A. 1963. *Animal Ecology: Aims and Methods*. 2nd ed. Sir Isaac Pitman & Sons, London. 344 pp.

A good ecology text that emphasises the soil ecosystem. Approx. 1000 refs.

Murphy, P.W. (Editor). 1962. *Progress in Soil Zoology*. Butterworths, London. 398 pp.

Technical papers about methods of extracting soil animals. Refs. after each presentation.

Pesson, P. (Editor). 1971. *Le vie dans les sols. Aspects Nouveaux. Etudes experimentales*. Gautier-Villars, Paris. x + 472 pp.

Comprehensive review of ecology of soil organisms with emphasis on current research. Refs. after each chapter.

Phillipson, J. (Editor). 1971. *Methods of study in quantitative soil ecology: Population, production and energy flow*. I.B.P. Handbook No. 18. 297 pp. Blackwell, Oxford.

Good overview of current techniques. Refs. after each presentation.

Pimental, R.A. 1967. *Invertebrate Identification Manual*. Van Nostrand Reinhold Co., New York. 151 pp.

Excellent illustrations of the major orders and families.

Richards, B.N. 1974. *Introduction to the Soil Ecosystem*. Longman Inc., New York. 266 pp.

A good modern approach to the subject, from Australia. Refs. after each chapter.

Savory, T. 1971. *Biology of the Cryptozoa*. Merrow Publishing Co., Watford, England. 56 pp.

Introductory textbook.

Schaller, F. 1968. *Soil Animals*. Univ. Mich. Press, Ann Arbor. 145 pp.

Introduction to soil ecosystems, emphasizing larger soil animals. No references.

Sheals, J.G. (Editor). 1969. *The Soil Ecosystem*. Systematics Assoc., London. 247 pp.

Proceedings of conference emphasising problems of classification of soils and their components. Includes review on impacts of agricultural practices. Refs. after each presentation.

U.N.E.S.C.O. 1969. *Soil Biology: Review of Research*. U.N.E.S.C.O., Paris. 244 pp.

Summarizes knowledge of soil biological processes. Refs. after each chapter.

Vaněk, J. (Editor). 1975. *Progress in Soil Zoology*. Proceedings of the 5th International

Colloquium on Soil Zoology held in Prague, September 17–22, 1973. Academia Publishing House, Prague. 630 pp.

Most recent text on research in soil zoology as of 1975. Section on influence of human activities on soil organisms. Refs. after each presentation.

Wallwork, J.A. 1970. *Ecology of Soil Animals*. McGraw-Hill, New York. 283 pp.

Basic text updating some of the material in Kevan (1962). Refs. after each chapter.

Wallwork, J.A. 1976. *The Distribution and Diversity of Soil Fauna*. Academic Press, London. 355 pp.

A continuation of his *Ecology of Soil Animals* (1970). Refs. after each chapter.

Webb, J.E., J.A. Wallwork and J.H. Elgood. 1978. *Guide to Invertebrate Animals*. 2nd ed. Macmillan Press Ltd., London. 305 pp.

Guide for undergraduates with up-to-date classification scheme. Limited illustrations.

PROTOZOA

MacKinnon, D.L. and R.S.T. Hawes. 1961. *An Introduction to the Study of Protozoa*. University Press, Oxford.

Good section about methods.

Stout, J.D. and O.W. Heal. 1967. Protozoa. pp. 149–195. *In* Burges, N.A. and F. Raw. (Editors). *Soil Biology*. Academic Press, New York.

Excellent reference text on soil protozoa.

PLATYHELMINTHES

Schmidt, G.D. 1982. Platyhelminthes. pp. 727–823. *In* Parker, S.P. (Editor). *Synopsis and classification of living organisms*. Vol. 1. McGraw-Hill Book Co.

Primarily parasitic, some platyhelminthes are free-living in highly organic moist soils.

GASTROTRICHA

Hummon, W.D. 1982. Gastrotricha. pp. 857–863. *In* Parker, S.P. (Editor). *Synopsis and classification of living organisms*. Vol. 1. McGraw-Hill Book Co.

ROTIFERA

Donner, J. 1966. *Rotifers*. Frederick Warne & Co., Ltd., London. 80 pp.

Simple, yet thorough introduction to “wheel animals”. Mainly aquatic. 29 refs.

Nogrady, T. 1982. Rotifera. pp. 865–872. *In* Parker, S.P. (Editor). *Synopsis and classification of living organisms*. Vol. 1. McGraw-Hill Book Co.

Up-to-date classification of this group.

NEMATOMORPHA

Maggenti, A.R. 1981. *General Nematology*. Springer Verlag, New York. 372 pp.

Contains a short (pp. 27–32) section on Nematomorpha or gordian worms.

NEMATODA (= NEMATATA)

Bird, A.F. 1971. *The Structure of Nematodes*. Academic Press, New York. 318 pp.

General textbook on the morphology and physiology of nematodes.

Chitwood, B.G. and M.B. Chitwood. (Editors). 1950. *Introduction to Nematology*. University Park Press, London. 334 pp.

Papers on morphology, physiology and life histories.

Croll, N.A. 1970. *The Behaviour of Nematodes, their activity, senses and responses*. Edward Arnold Ltd., London. 117 pp.

Croll, N.A. and B.E. Matthews. 1977. *Biology of Nematodes*. John Wiley and Sons, New York, Toronto. 201 pp.

Introductory textbook presenting a unified view of the whole range of nematode types.

- Goodey, J.B. 1963. *Laboratory Methods for Work with Plant and Soil Nematodes*. 3rd ed. Ministry of Agriculture, Fisheries & Food (Tech. Bull. 2), London. 47 pp.
- Maggenti, A.R. 1981. *General Nematology*. Springer Verlag, New York. 372 pp.
Excellent general textbook on nematode morphology, physiology and classification. Third of book deals with parasitic types, no special section on free-living soil nematodes.
- Maggenti, A.R. 1981. *Nemata*. pp. 879–929. *In* Parker, S.P. (Editor). *Synopsis and classification of living organisms*. Vol. 1. McGraw-Hill Book Co.
Up-to-date classification of group.
- Nicholas, W.L. 1975. *The Biology of Free-Living Nematodes*. Clarendon Press, Oxford. 219 pp.
“This is a book written by an enthusiast for the unconvinced” and covers the morphology, physiology, biochemistry, ecology, culturing, techniques and introductory taxonomy of these invertebrates.
- Poinar, G.O., Jr. 1983. *The Natural History of Nematodes*. Prentice-Hall Inc., New Jersey. 323 pp.
Introductory textbook to biology and ecology of nematodes. Includes section on classification.
- Sasser, J.N. and W.R. Jenkins. (Editors). 1960. *Nematology: Fundamentals and recent advances with emphasis on plant parasitic and soil forms*. University of North Carolina Press, Chapel Hill, N.C. 480 pp.
Contains an excellent section on methodology.
- Southey, J.F. (Editor). 1959. *Plant Nematology*. Ministry of Agriculture, Fisheries & Food (Tech. Bull. 7), London. 175 pp.
Lecture course, which reviews the subject and emphasizes problems in British agriculture. Refs. after each chapter.
- Southey, J.F. (Editor). 1970. *Laboratory Methods for Work with Plant and Soil Nematodes*. Ministry of Agriculture, Fisheries & Food (Tech. Bull. 2), London. 148 pp.
A great “how-to” book on methods of studying nematodes.
- Thorne, G. 1961. *Principles of Nematology*. McGraw-Hill Book Co., New York, Toronto, London. 553 pp. 31 pp. refs.
- ANNELIDA (OLIGOCHAETA)*
- Anonymous. 1982. *Earthworms: Raising, uses, beneficial aspects 1978–1981*, 97 citations. Produced from AGRICOLA database. Available free from U.S.D.A. Library, Beltsville, MD.
- Appelhof, M. (Editor). 1981. *Workshop on the Role of Earthworms in the Stabilization of Organic Residues*. Vol. 1. Kalamazoo, Michigan, April 9–12, 1980. Beech Leaf Press, Kalamazoo, Michigan. 315 pp.
Has no bearing on identification but, besides being interesting, this book has an extensive list of research needs in Appendix.
- Bal, L. 1982. *Zoological Ripening of Soils*. Centre for Agricultural Research and Documentation, Wageningen, Netherlands. Agricultural Research Reports 850.
A monograph on the contribution of soil animals to soil structure, in which earthworms have an important role. The stilted text is redeemed by a number of excellent photographs, a glossary and a large bibliography.
- Bouché, M.B. 1972. *Lombriciens de France: Ecologie et systématique*. *Ann. Zool. Ecol. Anim.* 72(2): 214–472.

- Darwin, C. 1897. The formation of vegetable mould, through the action of worms with observations on their habits. John Murray, London. vii + 328 pp.
As relevant today as in 1897. There have been several reprintings. Darwin was one of the first to realise (and put his thoughts and painstaking observations into print) how earthworms affect the landscape. His estimates of earthworm (*L. terrestris*) density are probably low. Refs. throughout text.
- Edwards, C.A. and J.R. Lofty. 1972. Biology of Earthworms. Chapman & Hall, London. 283 pp.
Comprehensive review of all aspects of earthworm biology and ecology. 32 pp. of refs. 2nd edition in 1977 with a more complete bibliography.
- Gates, G.E. 1972. Burmese Earthworms. An introduction to the systematics of megadrile oligochaetes with special references to Southeast Asia. Trans. Amer. Philos. Soc. 62(7): 1-326.
- Lee, K.E. 1959. The Earthworm Fauna of New Zealand.. N.Z. Dept. Scientific & Industrial Research, Auckland. 486 pp.
Has general application.
- Nielsen, C.O. and B. Christensen. 1959, 1961, 1963. The Enchytraeidae: Critical Revision and Taxonomy of European Species. *Natura Jutlandica*. Vols. 8, 9, 10.
Essential for workers on Enchytraeidae.
- Reynolds, J.W. 1977. The Earthworms (Lumbricidae and Sparganophilidae) of Ontario. Royal Ontario Museum, Life Sciences, Misc. Publications. 141 pp.
A comprehensive review of the Ontario earthworm fauna. Very well illustrated by Dan Dindal. Indispensable for Ontario workers. Good bibliography with the bonus that Reynolds cites his and Gates' papers in the Bull. Tall Timbers Res. Stn. and Megadrilologica up to 1977. Reynolds has published extensively on the earthworm fauna of several American states (particularly in the Northeast) and several Canadian provinces (Ontario, Quebec, Nova Scotia, New Brunswick, and P.E.I.). This book also briefly summarizes Reynolds' considerable experience in sampling methods and preservation of earthworm specimens.
- Satchell, J.E. (Editor). 1983. Earthworm Ecology. Chapman & Hall Ltd., London. 495 pp.
Papers cover topics under the general headings of: earthworms and organic matter; earthworm ecology in grassland soils, in cultivated soils, in forest soils, in tropical and arid soils; earthworms and land reclamation, and soil pollution; utilization of wastes by earthworm culture; earthworms and microflora; earthworms in food chains; earthworm evolution and distribution patterns; taxonomy and nomenclature. Refs. after each chapter.
- Sims, R.W. In press. A Classification and the Distribution of Earthworms, Suborder Lumbricina (Haplotaxida: Oligochaeta). Bull. Brit. Mus. Nat. Hist. (Zool.).
- Worden, D.D. (Editor). 1981. Workshop on the Role of Earthworms in the Stabilization of Organic Residues. Vol. II. Bibliography. Beech Leaf Press, Kalamazoo, Michigan.
3036 citations, cumulative author and subject indices. Nematodes and microorganisms that impact on earthworms are also cited.
- Zajonc, I. and J. Cepelak. 1968. Colloquium - Questions on Ecology and Taxonomy of Earthworms. 149 pp. Institute of Zoology - Institute for Biology and Ecology of Cultural Plants, Agricultural University, Nitra, Czechoslovakia. 149 pp.
Papers in English, French, German, Russian. Refs. after each presentation.

MOLLUSCA

- Cameron, R.A.D. and M. Redfern. 1976. British Land Snails. Synopses of the British Fauna

(New Series) No. 6. Publ. for Linnean Soc. of London by Academic Press, London. 64 pp.
Keys and notes to the identification of species. Contains sections on morphology, collecting and preservation.

Leonard, A.B. 1959. Handbook of Gastropods of Kansas. University of Kansas Natural History Museum, Topeka, Kansas.

Only partially applicable to Canada.

Runham, N.W. and P.J. Hunter. 1970. Terrestrial Slugs. Hutchinson University Library, London. 185 pp.

Review of biology, ecology and economic importance of slugs. 21 pp. of refs.

CRUSTACEA

Bousfield, E.L. 1982. Amphipoda. pp. 254–293. In Parker, S.P. (Editor). Synopsis and classification of living organisms. Vol. 2. McGraw-Hill Book Co.

Crustaceans common in tropical soils.

Richardson, H. 1905. A Monograph on the Isopods of North America. Bull. U.S.N.M. 54: Reprinted by Antiquariaat Junk, Netherlands 1972.

A classic, and still useful.

Schultz, G.A. 1982. Isopoda. pp. 249–254. In Parker, S.P. (Editor). Synopsis and classification of living organisms. Vol. 2. McGraw-Hill Book Co.

Up-to-date classification of Woodlice.

Sutton, S.L. 1972, 1980. Woodlice. Ginn & Co., Ltd., London. 144 pp.

An introduction to the biology, ethology, genetics, ecology, and identification of woodlice. Includes a section on techniques.

Walker, E.M. 1927. The Woodlice or Oniscoidea of Canada (Crustacea, Isopoda). Can. Field - Nat. 41: 173–179.

Van Name, W.G. 1936. The American Land and Freshwater Isopod Crustacea. Bull. Am. Mus. Nat. Hist. 71: 1–535.

Useful for identifying Canadian species.

TARDIGRADA

Morgan, C.I. 1982. Tardigrada. pp. 731–739. In Parker, S.P. (Editor). Synopsis and classification of living organisms. McGraw-Hill Book Co.

Up-to-date classification of group.

MYRIAPODA

Blower, J.G. 1958. British Millipedes (Diplopoda). Linnean Soc. Synopses of the British Fauna, 11: 74 pp.

Mainly taxonomic; useful in E. Canada where most species are European introductions.

Blower, J.G. (Editor). 1974. Myriapoda. Symposia of the Zoological Society of London, 32. Academic Press, London & New York. 712 pp.

General work, including some taxonomy.

Broleman, H.W. 1932. Chilopodes. Faune France 25. 405 pp.

Useful for the numerous introduced species.

Demange, J.-M. 1981. Les Mille-Pattes, Myriapodes. Société Nouvelle des Editions Boubée, Paris. 284 pp.

Morphology, ecology and ethology of class with key to determination to species of myriapods in France. Excellent figures plus 4 plates in colour and 9 colour photographs.

Eason, E.H. 1964. Centipedes of the British Isles. Frederick Warne & Co., Ltd., London. 294 pp.

- Has general application; useful in E. Canada where most species are the same or similar.
- Edwards, C.A. 1952. A Revision of the British Symphyla. *Proc. Zool. Soc. London*. 132: 403–439.
- Edwards, C.A. 1952. Keys to the Genera of the Symphyla. *J. Linn. Soc. Zool.* 44: 164–169.
- Most useful text on Symphyla.
- Hoffman, R.L. 1979. Classification of the Diplopoda. *Muséum d'Histoire Naturelle, Genève*. 237 pp.
- Hoffman, R.L. 1982. Chilopoda. pp. 681–688 *In* Parker, S.P. (Editor). *Synopsis and classification of living organisms*. Vol. 2. McGraw-Hill Book Co.
- Most recent classification of centipedes.
- Hoffman, R.L. 1982. Diplopoda. pp. 689–724. *In* Parker, S.P. (Editor). *Synopsis and classification of living organisms*. Vol. 2. McGraw-Hill Book Co.
- Most recent classification of millipedes.
- Kevan, D.K.McE. 1983a. A Preliminary Survey of Known and Potentially Canadian and Alaskan Centipedes (Chilopoda). *Can. J. Zool.* 61: 2938–2955.
- Present state of knowledge of centipedes, in Canada and Alaska, including economic and biological aspects. Excellent reference section.
- Kevan, D.K.McE. 1983b. A Preliminary Survey of Known and Potentially Canadian and Alaskan Millipedes (Diplopoda). *Can. J. Zool.* 61: 2956–2975.
- Diplopod fauna of Canada, including a checklist of species known to, and likely to occur, in Canada. Excellent reference section.
- Lewis, J.G.E. 1981. *The Biology of Centipedes*. Oxford University Press. 476 pp.
- Most recent textbook on this subject.
- Remy, P.A. 1958. *Paupodes des Etats-Unis d'Amerique et de la Jamaïque*. *Mém. Soc. Natn. Sci. nat. math. Cherbourg* 48. 77 pp.
- Probably will be useful for some Canadian species.
- Scheller, U. 1982. Pauropoda. pp. 724–726. *In* Parker, S.P. (Editor). *Synopsis and classification of living organisms*. Vol. 2. McGraw-Hill Book Co.
- Up-to-date classification of pauropods.
- Scheller, U. 1984. Pauropoda (Myriapoda) from Canada. *Can. J. Zool.* In press.
- COLLEMBOLA**
- Christiansen, K. and P. Bellinger. 1980–1981. *The Collembola of North America North of Rio Grande*. Part 1 (1980) Poduridae and Hypogastruridae. Part 2 (1980) Onychiuridae and Isotomidae. Part 3 (1980) Entomobryidae. Part 4 (1981) Neelidae and Sminthuridae. 1322 pp. Grinnell College, Grinnell.
- The current standard work on North American Collembola. Illustrations are numerous, but finer details are obscured by bad printing. Part 1 contains a good general description of Collembola morphology and describes several slide preparation techniques. Part 4 contains a useful morphological glossary and an exhaustive author index.
- DeHarveng, L. 1982. Clé de détermination des genres de Neanurinae (Collemboles) d'Europe et de la région Méditerranéenne avec description de deux nouveaux genres. *Trav. Lab. Ecobiol. Arthr. Edaph.*, Toulouse 3(4): 7–13.
- Identification keys to the many new Neanurinae genera described from Europe since Gisin (1960).
- Ellis, W.N. & P.F. Bellinger. 1973. An annotated list of generic names of Collembola (Insecta) and their type species. *Mon. Ned. Ent. Ver.* 7: 1–74.

A necessary publication for taxonomists in particular.

Fjellberg, A. 1980. Identification keys to Norwegian Collembola. Norsk Entomologisk Forening, As. 152 pp.

Fairly up to date, illustrated keys covering most of the Nordic species.

Fjellberg, A. 1984. Arctic Collembola 1. Alaskan Collembola of the families Poduridae, Hypogastruridae, Odontellidae, Brachystomellidae and Neanuridae. Ent. Scand. Suppl. (In press).

Gisin, H. 1960. Collembolenfauna Europas. Museum d'Histoire Naturelle, Genève. 312 pp.

Well illustrated identification keys and short description of species. Contains a general introduction to collembole morphology and identification technique. Although largely out of date, the book is still the standard work among European collembologists.

Massoud, A. 1967. Monographies des Neanuridae, Collemboles Poduromorphes a pièces buccales modifiées. Biol. Amer. Austr. CNRS 3: 1–399.

A standard work on the family Neanuridae, but now largely out of date, at least concerning the European fauna.

Maynard, E.M. 1951. A Monograph of the Collembola or Springtail Insects of New York State. Comstock Publishing Co. Inc., Ithaca, NY. 339 pp. + 29 pl.

A few biological notes included; nomenclature not up to date.

Rusek, J. 1977. Protura, Collembola, Diplura, Thysanura. Enumeration Insectorum Bohemoslovakiae. Acta Faun. Ent. Mus. Nat. Pragae 15(4): 9–21.

A check list to the apterygotan species recorded from Czechoslovakia.

Salmon, J.T. 1964. An Index to the Collembola. Bull. Roy. Soc. New Zealand 7(1–2). 644 pp. Wellington.

An index to world literature on Collembola up to 1962 arranged (1) by author and (2) by species. Contains also a key to world genera. A very useful book despite numerous minor errors.

Yosii, R. 1977. Critical check list of the Japanese species of Collembola. Contr. Biol. Lab. Kyoto University 25(2): 141–170.

In addition to the species list, the paper also provides identification keys to the Japanese genera.

INSECTS (OTHER THAN COLLEMBOLA)

Arnett, R.H. Jr., N.M. Downie and H.E. Jaques. 1980. How to Know the Beetles. Brown Publishing Co., Dubuque. 416 pp.

Chandler, L. 1957. The orders Protura and Diplura in Indiana. Proc. Indiana Acad. Sci. 66: 112–114.

Of very limited use.

Chu, H.F. 1949. How to know the immature insects. Brown Publishing Co., Dubuque. 234 pp.

Lee, K.G. & T.G. Wood. 1971. Termites and Soils. Academic Press, London and New York.

Morgan, C.I. and P.E. King. 1976. British Tardigrades, Tardigrada: Keys and notes for the identification of the species. Synopsis of the British Fauna No. 9. Academic Press, London. 133 pp.

Important reference source.

Nosek, J. 1973. The European Protura. Museum d'Histoire Naturelle, Genève. 345 pp.

The most up-to-date work on taxonomy, ecology and distribution. Includes keys for identification.

Ramazzotti, G. 1972. Il Phylum Tardigrada. Mem. Ist Ital. Idrobiol. 28: 1–732.

An introduction to the world literature on the group.

Smith, L.M. 1960. The family Projapygidae and Anahapygidae (Diplura) in North America. *Ann. Ent. Soc. Am.* 53: 575–583.

Sudd, J.M. 1967. An introduction to the behaviour of ants. Edward Arnold Ltd., London.
A useful introduction to ants.

Tuxen, S.L. 1964. The Protura. A revision of the species of the world with keys for determination. Hermann, Paris. 360 pp.

A major work on Protura.

ARACHNIDA (EXCEPT ACARI)

Comstock, J.H. 1940. The Spider Book. Cornell University Press, Ithaca, NY. 727 pp.

A classic spider work, though outdated taxonomically.

Gertsch, W.J. 1978. American Spiders. 2nd ed., Van Nostrand-Reinhold, New York. (1st ed. 1949).

A readable summary for general readers.

Hoff, C.C. 1949. The Pseudoscorpions of Illinois. *Illinois Nat. Hist. Surv. Bull.* 24: 412–498.

A somewhat dated, but still very useful, introduction to morphology and key.

Hoff, C.C. 1958. List of the Pseudoscorpions of North America North of Mexico. *Amer. Mus. Nov. No.* 1875: 1–50.

With a key to genera.

Hoff, C.C. 1959. The Ecology and Distribution of the Pseudoscorpions of North-Central New Mexico. University of New Mexico Publications in Biology, No. 8. 68 pp.

Contains much general information on biology.

Kaston, B.J. 1948. Spiders of Connecticut. *Bull. Conn. Geol. Nat. Hist. Surv.* 70: 1–874.

A classic study, very useful for northeastern U.S. and southeastern Canada. Supplement published in 1977 (*Jour. Arachnol.* 4: 1–72) updates nomenclature and selected keys.

Kaston, B.J. 1972. How to Know the Spiders. 3rd ed., W. Brown, Dubuque. 272 pp.

Collection techniques, picture keys to orders and families and keys to most common genera; a good place to start.

Levi, H.W., L.R. Levi and H.S. Zim. 1968. A Guide to Spiders and Their Kin. Golden Press, New York. 160 pp.

A non-technical, "look-see" guide.

Muchmore, W.B. 1982. Pseudoscorpionida. pp. 96–102. *In* Parker, S.P. (Editor). Synopsis and classification of living organisms. Vol. 2. McGraw-Hill Book Co.

Nelson, S. Jr. 1975. A Systematic Study of Michigan Pseudoscorpionida (Arachnida). *Amer. Midl. Nat.* 93: 257–301.

Savory, T. 1977. Arachnida. 2nd ed. Academic Press, London, New York. 340 pp.

General introduction to the morphology, physiology, ecology, and taxonomy of the class.

Weygoldt, P. 1969. The Biology of Pseudoscorpions. Harvard University Press, Cambridge, MA. 145 pp.

Translation from German of 1966. Covers anatomy, physiology, ecology, taxonomy and techniques. An excellent, readable summary.

ACARI

Baker, E.W. and G.W. Wharton. 1952. An Introduction to Acarology. The Macmillan Co., New York. 465 pp.

Largely but not exclusively taxonomic.

Balogh, J. 1972. The Oribatid Genera of the World. Akad. Kiado, Budapest. 188 pp. + 71 pls.

- Balogh, J. and S. Mahunka. 1983. *The Soil Mites of the World. 1. Primitive Oribatids of the Palaearctic Region*. Elsevier, Amsterdam. 372 pp.
Keys to Palaearctic species.
- Evans, G.O., J.G. Sheals, & D. MacFarlane. 1961. *The Terrestrial Acari of the British Isles: An Introduction to their Morphology, Biology and Classification*. British Museum, London. 219 pp.
- Evans, G.O. and W.M. Till. 1979. Mesostigmatic Mites of Britain and Ireland (Chelicerata: Acari-Parasitiformes). *Trans. Zool. Soc. Lond.* 35: 139–270.
An introduction to their external morphology and classification.
- Gilyarov, M.S. (Editor). 1975. *A Key to the Soil-inhabiting Mites, Sarcoptiformes*. (In Russian). Nauka, Moscow. 491 pp.
Translation (on fiche) available from Canadian Index of Scientific Translations, Canada Institute for Scientific and Technical Information, National Research Council of Canada, Ottawa K1A 0S2. (Translation #4328).
- Gilyarov, M.S. 1978. *A Key to the Soil-inhabiting Mites, Trombidiformes*. (In Russian). Nauka, Moscow.
Relevant to North American fauna. Translation available as per Gilyarov (1975). (Translation #4569).
- Gilyarov, M.S. and N.G. Bregetova. (Editors). 1977. *A Key to the Soil-inhabiting Mites, Mesostigmata*. (In Russian). Nauka, Leningrad. 718 pp.
Very relevant to North American fauna. Translation available as per Gilyarov (1975). (Translation #4371).
- Hughes, T.E. 1959. *Mites, or the Acari*. University of London Athlone Press, London. 225 pp.
- Kethley, J. 1982. Acariformes – Prostigmata. pp. 117–145. *In* Parker, S.P. (Editor). *Synopsis and classification of living organisms*. Vol. 2. McGraw-Hill Book Co.
- Krantz, S.W. 1978. *A Manual of Acarology*. Oregon State University, Corvallis, OR. 509 pp. 2nd ed.
Largely, but not exclusively, taxonomic. The most widely used introductory text on acarology.
- O'Connor, B.M. 1982. Astigmata. pp. 146–169. *In* Parker, S.P. (Editor). *Synopsis and classification of living organisms*. Vol. 2. McGraw-Hill Book Co.
- NOTE: A manual dealing with soil organisms in North America is presently being edited by D.L. Dindal (to be published by J. Wiley & Sons).

STATISTICS, EXPERIMENTAL DESIGN & SAMPLING TECHNIQUES FOR SOIL ZOOLOGY

Unlike the epigeic fauna, there are few “models” which have been explicitly established for soil animal populations. Many epigeic models have been adapted for soil animal models with varying degrees of success. The euedaphic fauna is rarely homogeneous even throughout the small volumes of sampling cores; the fauna varies dramatically with depth and is highly dependent upon climate factors, soil type, vegetation cover and, structures as roots or earthworm tunnels, for example. Soil animals often exhibit aggregative behaviour, which, presumably, is their response to exploitation of food resources (which again are often aggregated and not evenly or even randomly dispersed in a plot) or reproductive requirements. There are a large number of statistical texts available for consultation for the more difficult

statistical analyses, and the wide availability of computers often makes it tempting to get heavily (perhaps even unnecessarily) involved in this end of the work. An appraisal of statistical texts is not provided, but listed are a few texts and papers which have an ecological bent, and that are useful in accessing and comprehending this literature. The assistance of a *sympathetic* biometrician for assistance in field experiments should not be underrated.

Marked-capture-recapture techniques, which should have some utility for estimating the abundance of soil animal populations, have not been widely used in the past for this purpose, but these techniques might be particularly applicable to earthworms, for example. Some of the listings given provide numbers and analyses of soil faunal data on which to hang your hat or against which you may compare your own data.

Gauch, H.G., Jr. *ca.* 1976–present. The Cornell Ecology Programs Series. Available from Cornell University, Dept. of Ecology & Systematics, 224 Langmuir Laboratory, Ithaca, NY 14850.

A series of main-frame computer programs (with considerable documentation) for analysing ecological data. The catalog has been revised and up-dated several times. Program & documentation are available at nominal cost. Several Canadian universities and government institutions now provide and support these programs. The programs deal mainly with ordination and classification of data (particularly useful for large sets of data).

Jeffers, J.N.R. Statistical Checklists. Nos. 1, 2, & 3 (Design of Experiments, Sampling & Modelling, respectively). Institute of Terrestrial Ecology, Cambridge, UK.

Lists of questions to ask of yourself and your experiments. Thought-provoking and helpful.

Jeffers, J.N.R. 1978. An Introduction to Systems Analysis with Ecological Applications. University Park Press, Baltimore.

For those of you into ecological modelling - this is a very readable account with lots of worked examples.

Lewis, T. and L.R. Taylor. 1967. Introduction to Experimental Ecology. Academic Press.

A relatively basic approach to quantitative ecology, but a treasury of techniques, graphs, lists and analytical methodology for ecologists.

Macfadyen, A. 1963. Animal Ecology. 2nd Ed. Pitman & Sons.

Less mathematical approach than Southwood or Taylor & Lewis, but Macfadyen's credentials as a soil zoologist mean that there are plenty of illustrative examples from soil ecology.

Petersen, H. (Editor). 1982. Quantitative ecology of microfungi and animals in soil and litter. *Oikos* 39: 388–422.

Extensive tabulations and comparisons of various components of the soil fauna for various global biomes and their impact on decomposition and soil processes. An invaluable aid for comparison purposes and highlighting the many deficiencies.

Phillipson, J. (Editor). 1971. Methods of Study in Quantitative Soil Ecology. Blackwell Scientific Publications. IBP Handbook No. 18.

A comprehensive account of various soil animal sampling techniques. An indispensable handbook for this type of work. Phillipson's final chapter on "Other Arthropods" is brief but helpful entree to many of these neglected taxa (*e.g.*, Tardigrada).

Pielou, E.C. 1976. *Mathematical Ecology*. John Wiley & Sons.

A very mathematical (not statistical) approach to ecology. Heavy going in many places. A source book for the mathematically-minded ecologist.

Seber, G.A.F. 1973. *The Estimation of Animal Abundance and Related Parameters*. Hafner Press, New York.

Very heavy going in places, but a comprehensive review of various sampling and marked-capture-recapture techniques. The final chapter is an excellent summary of methods discussed in the book.

Southwood, T.R.E. 1978. *Ecological Methods*. 2nd Ed. Chapman & Hall.

A somewhat more sophisticated approach than Lewis & Taylor, but otherwise comparable. Excellent bibliographies.

Wallwork, J.A. 1970. *Ecology of Soil Animals*. McGraw-Hill.

The best single "read" on the details of soil ecology from concepts to specimen preservation. Good bibliographies. There is a brief section on extraction techniques for soil animals. References are now somewhat dated.

Wallwork, J.A. 1976. *The Distribution and Diversity of Soil Fauna*. Academic Press.

Lots of relevant goodies here. Written by a soil ecologist specializing in soil mites. Chapter 2 is a "quickie" review of statistical and measuring techniques and ecological concepts. Highly recommended.

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